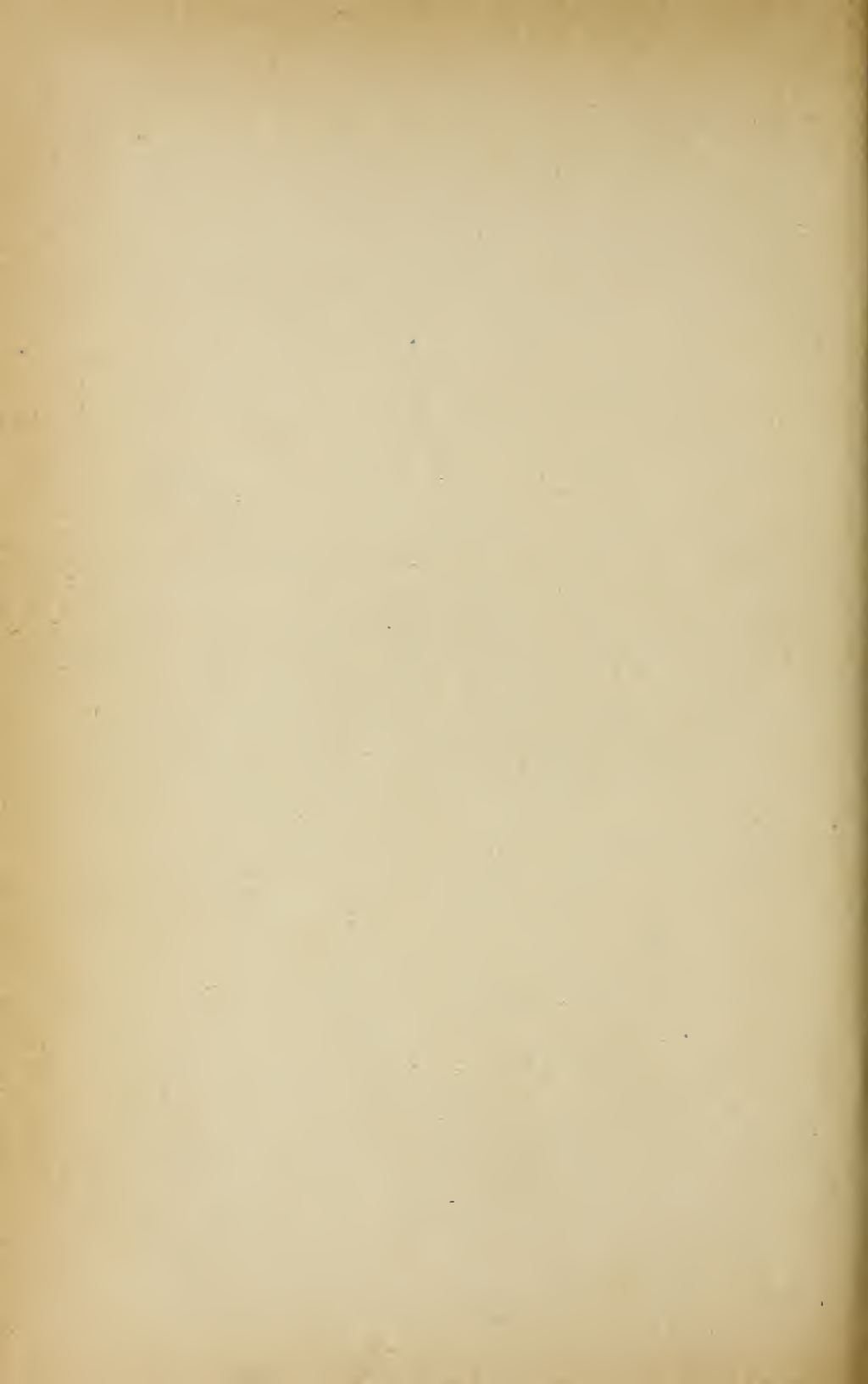


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U. S. DEPARTMENT OF AGRICULTURE
DIVISION OF ORNITHOLOGY AND MAMMALOLOGY

NORTH AMERICAN FAUNA

No. 12

[Actual date of publication, July 23, 1896.]



GENERA AND SUBGENERA OF VOLES AND LEMMINGS

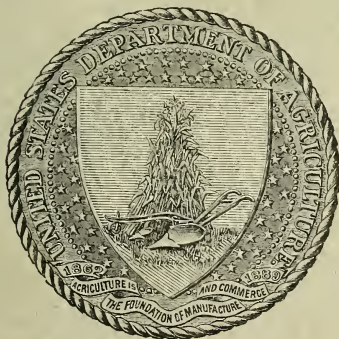
BY

GERRIT S. MILLER, Jr.

Prepared under the direction of

Dr. C. HART MERRIAM

CHIEF OF DIVISION OF ORNITHOLOGY AND MAMMALOLOGY



WASHINGTON
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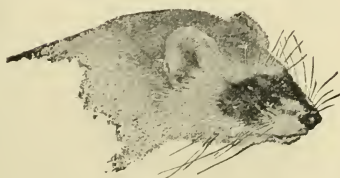
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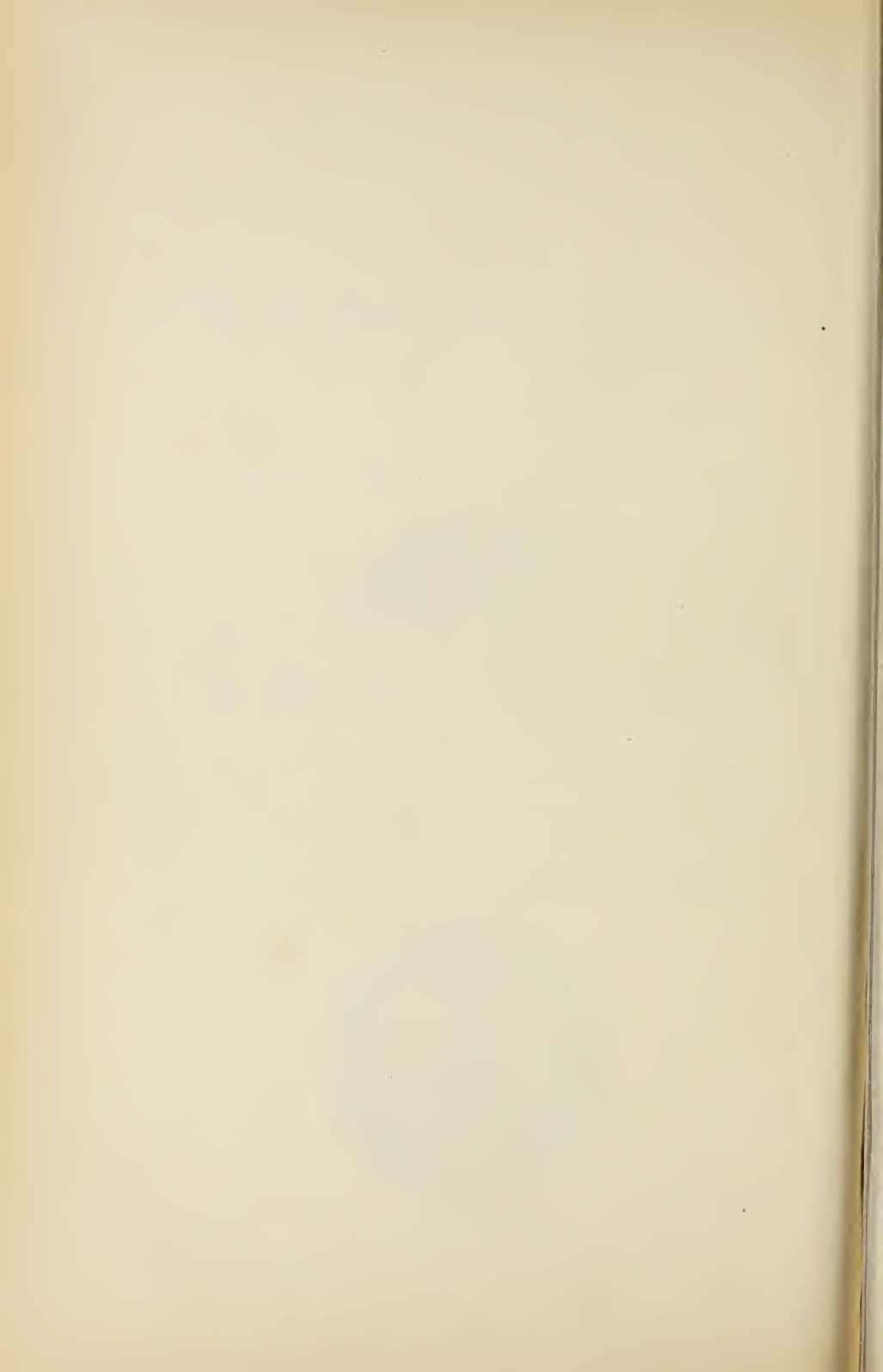
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LETTER OF TRANSMITTAL.

UNITED STATES DEPARTMENT OF AGRICULTURE,
DIVISION OF ORNITHOLOGY AND MAMMALOGY,
Washington, D. C., May 12, 1896.

SIR: I have the honor to transmit herewith, and recommend for publication, the manuscript of No. 12 of North American Fauna, treating of the Genera and Subgenera of Voles and Lemmings, and comprising results of investigations carried on in the Division of Ornithology and Mammalogy by Gerrit S. Miller, jr.

Respectfully,

C. HART MERRIAM,
Chief of Division.

Dr. CHAS. W. DABNEY, Jr.,
Acting Secretary of Agriculture.



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THE GENERA AND SUBGENERA OF VOLES AND LEMMINGS.

By GERRIT S. MILLER, JR.

The following revision of the genera and subgenera of voles and lemmings is chiefly the result of a study made in the Division of Ornithology and Mammalogy of the collections belonging to the United States Department of Agriculture. This material has been supplemented by specimens from my own private collection and those of Mr. Outram Bangs, Mr. S. N. Rhoads, and Dr. C. Hart Merriam. I have also had access to the voles and lemmings in the American Museum of Natural History, the United States National Museum, and the British Museum. Thanks are due to all who have placed material at my disposal, and especially to Mr. Oldfield Thomas, curator of mammals in the British Museum.

Hitherto no attempt has been made to compare in detail the voles and lemmings of the Old and New Worlds. This is the necessary result of the poor quality and small number of specimens from the opposite side of the Atlantic to be found in museums and private collections in both Europe and America. In consequence of this lack of material, writers who have been thoroughly acquainted with indigenous voles and lemmings have either made no comparison of these with exotic forms, or have reached faulty or at least incomplete conclusions with regard to groups occupying widely separated geographic regions.

For determining the relationships of the different voles and lemmings the collection in the British Museum offers exceptional facilities. It contains representatives of all the recent genera and subgenera found in the Old World, and lacks only one of those peculiar to America. The collection is, moreover, especially rich in specimens identified by the more prominent writers on the subject—a circumstance of the utmost importance.

The drawings for the illustrations in this paper, except fig. 9 and Pls. I and II, were made under my constant supervision by Mr. F. Müller. Pls. I and II were prepared by Dr. James C. McConnell. Figs. 4, 5, 8, and 10 of Pl. II were drawn in ink by Dr. McConnell from pencil drawings made at the British Museum by Mr. Hollick. Fig. 7 of the same plate is by Dr. McConnell from a pencil drawing by Mr. A.

Westergren. The tracings of the enamel pattern of *Microtus luteus* and *M. lagurus* are enlarged from figs. 10, 11, 15, and 16 of Pl. XIII of Büchner's 'Wissenschaftliche Resultate der von N. M. Przewalski nach Central-Asien unternommenen Reisen.' In fig. 22 the enamel patterns of the front lower molar and middle and back upper molars are enlarged from Mr. Hollick's pencil drawing of a specimen from Fokien, China (British Museum Register 92. 10. 12. 52), the other teeth from fig. 1, Pl. XLVI of Milne-Edwards's 'Recherches pour servir à l'Histoire Naturelle des Mammifères.' Fig. 23 is compounded in the same way from Mr. Hollick's drawing and the original figure published by Thomas.

THE SUBFAMILY MICROTINÆ AND ITS MAIN DIVISIONS.

The subfamily *Microtinæ*¹ is a group of murine rodents closely related to the *Neotomina*, *Cricetina*, and *Myotalpina*.² It is distinguished from the first and second by cranial and dental characters; from the last chiefly by peculiarities in external form.³ While it is not the purpose of the present paper to discuss the relationships of the *Microtinæ* to any of these, it is important to consider in some detail the larger divisions of the subfamily itself before taking up the genera and subgenera.

The members of the subfamily *Microtinæ* fall naturally into two supergeneric groups, the *Lemmi* and *Microti*, or lemmings and voles. The former includes the genera *Synaptomys*, *Lemmus*, and *Dicrostonyx*, the latter the genera *Phenacomys*, *Exotomys*, *Microtus*, and *Fiber*.

Lemmi.—Skull generally broad and massive; lower incisors short, with roots ending on inner side of molars (Pl. III, fig. 1); crowns of maxillary teeth scarcely, if at all, narrower posteriorly than anteriorly (figs. 10, 11, and 12); tail usually shorter than hind foot (in *Synaptomys* slightly longer); palms and soles usually without distinct tubercles.

Microti.—Skull comparatively slender and lightly built; lower incisors long, with roots ending on outer side of molars (Pl. III, figs. 2 and 3); crowns of maxillary teeth distinctly narrower posteriorly than anteriorly (figs. 17, 19, 21–35); tail usually much longer than hind foot (in the Asiatic species of *Lagurus* distinctly shorter); palms and soles always with distinct tubercles.

In external appearance the lemmings and voles differ considerably. The former are mostly thick-set animals, with powerful fossorial feet, long, dense fur and very short tails, while the latter are more slender, with longer tails and with the fur and feet not so highly modified.

¹ = *Arvicolina* Auct. This name, however, must be abandoned, together with the generic name *Arvicola* (see p. 14).

² = *Siphneina* Auct. As *Siphneus* (Brants, 1827) must give place to *Myotalpa* (Kerr, 1792) (see Allen, Bull. Am. Mus. Nat. Hist., New York, VII, p. 183, 1895) it is necessary to make a corresponding change in the name of the subfamily.

³ The characters separating the *Myotalpine* from the *Microtinæ* are of much less importance than those separating the latter from any of its other allies. So close, indeed, is the resemblance between the two that it may eventually prove necessary to unite them under one name. Lack of material prevents any final conclusion at present.

Although the voles and lemmings may usually be distinguished at a glance, there are certain genera and subgenera the exact position of which is not at first apparent. Thus the species of *Lagurus*, although voles, so closely resemble lemmings in external appearance that their true relationships have been only very recently detected. On the other hand, *Synaptomys*, a true lemming, has much the superficial appearance of certain forms of *Microtus*.

LIST OF GENERA AND SUBGENERA OF MICROTINÆ.

Genera.	Subgenera.	Types.
<i>Synaptomys</i> .		<i>Synaptomys cooperi</i> .
	<i>Mictomys</i> .	<i>Synaptomys innotatus</i> .
<i>Lemmus</i> .		<i>Lemmus lemmus</i> .
<i>Dicrostonyx</i> .		<i>Dicrostonyx torquatus</i> .
<i>Phenacomys</i> .		<i>Phenacomys intermedius</i> .
<i>Evotomys</i> .		<i>Evotomys rutilus</i> .
<i>Microtus</i> .		<i>Microtus arvalis</i> .
	<i>Eothenomys</i> .	<i>Microtus melanogaster</i> .
	<i>Antelionomys</i> .	<i>Microtus chinensis</i> .
	<i>Lagurus</i> .	<i>Microtus lagurus</i> .
	<i>Alticola</i> .	<i>Microtus stoliczkaanus</i> .
	<i>Hyperacrius</i> .	<i>Microtus fertilis</i> .
	<i>Phaiomys</i> .	<i>Microtus blythii</i> .
	<i>Pedomys</i> .	<i>Microtus austerus</i> .
	<i>Pitymys</i> .	<i>Microtus pinetorum</i> .
	<i>Chilotus</i> .	<i>Microtus oregoni</i> .
	<i>Microtus</i> .	<i>Microtus arvalis</i> .
	<i>Arvicola</i> .	<i>Microtus terrestris</i> .
	<i>Neofiber</i> .	<i>Microtus alleni</i> .
<i>Fiber</i> .		<i>Fiber zibethicus</i> .

The following groups are known to occur in both hemispheres:

<i>Lemmus</i> .	<i>Microtus</i> (genus and subgenus).
<i>Dicrostonyx</i> .	<i>Lagurus</i> .
<i>Phenacomys</i> ?	<i>Pitymys</i> .
<i>Evotomys</i> .	<i>Arvicola</i> .

The following groups have been found in the Old World only:

<i>Eothenomys</i> .	<i>Alticola</i> .
<i>Antelionomys</i> .	<i>Hyperacrius</i> .
<i>Phaiomys</i> .	

The following groups have been found in America only:

<i>Synaptomys</i> .	<i>Chilotus</i> .
<i>Mictomys</i> .	<i>Neofiber</i> .
<i>Pedomys</i> .	<i>Fiber</i> .

GEOGRAPHIC DISTRIBUTION.

The subfamily *Microtinæ* is distributed throughout the extratropical region of the Northern Hemisphere. In the north some members of the group approach the extreme limit of mammalian life, while in the south a few species enter the northernmost edge of the tropics. The subfamily, which is clearly boreal in origin, reaches its highest develop-

ment in temperate Europe, Asia, and North America. Although it is probable that no species are common to both continents, five genera and four subgenera of the genus *Microtus* have a circumpolar distribution. On the other hand, no genera are peculiar to the Old World, and only two are confined to America. Asia has five subgenera of *Microtus* not found in America, and America has three not known to occur in the Old World.

HABITS.

The voles and lemmings occur in great abundance throughout the region which they occupy. They live in an endless variety of situations, from sea beaches to marshes and Alpine mountain tops, and from open plains to the densest forests. They are, perhaps, most numerous in well-watered grass lands. In localities where they are abundant most of the species make their presence known by trails or runways traced through the vegetation near their burrows. Occasionally, however, they occupy hollows in decaying logs or among loose rocks, and use natural crevices instead of beaten paths. While the great majority of species spend much of their time on the surface, protected by the overhanging vegetation, a few live almost exclusively underground, and in consequence of this habit have acquired numerous modifications which fit them for the needs of a subterranean life. Others are amphibious and never occur at any great distance from water. At least one member of the subfamily¹ is said to live among the branches of trees. The food is chiefly vegetable, though most species occasionally eat animal food. The vegetable food consists principally of grass stems, though roots, bark, leaves, seeds, and fruit are at times eaten in varying quantities. As voles are readily caught in traps baited with meat, it is probable that flesh forms part of their normal food. Mollusks are eaten freely when they can be obtained.

The voles and lemmings breed very rapidly during the warmer part of the year. The number of young in a litter varies from one or two to ten. Five is, perhaps, the average number in the majority of species, though it is probably less in those in which the females have only four mammae.

¹ *Phenacomys longicauda* True, from Oregon. In the original description of the species (Proc. U. S. Nat. Mus., XIII, pp. 303-304, Nov. 15, 1890) Mr. True quotes as follows from a letter from Mr. Aurelius Todd, who collected the type specimen: "It lives exclusively, as far as I have been able to ascertain, among the boughs and branches of the Oregon pine trees (*Abies douglasi*), making a nest of a size smaller than a robin's nest. It is usually situated on the upper side of a medium-sized branch, perhaps 6 inches in diameter, and is composed of the leaves of the tree deftly split in two from one end to the other and dried. The nest is neatly and rather ingeniously made, and the sameness of the material is a novelty. * * * The mouse is almost exclusively arboreal in its habits, but I think that I have reason to believe that they sometimes come to the ground for food, as I have seen tracks in the snow around the trees which I think were made by these little animals. They could be tracked up and down the tree, but to no great distance from it, and were most likely in search of food."

The young are born in nests made of soft vegetable fibers. The nests are usually placed in a burrow or beneath shelter of some kind and vary with the size of the animals, but are usually about 200 mm. in diameter. The species of *Fiber* make nests containing several bushels of material. These are conspicuous objects in the marshes where the animals live. Under conditions the nature of which is not understood the rate of increase in certain species is occasionally so enormously accelerated that an area becomes overcrowded and the animals wander into the surrounding country in search of food. So far as known, such 'lemming migrations' and 'vole plagues' are phenomena peculiar to the Old World.¹

NOMENCLATURE.

Before considering the characters of the genera and subgenera of *Microtinae* it is necessary to examine a considerable part of the mass of technical literature to which, during the past hundred and forty years, the animals in question have given rise. Since Linnæus published the tenth edition of the *Systema Naturæ* more than fifty names have been used for the less than two dozen namable superspecific groups recognizable in the subfamily. In considering their claims to recognition the names may be best taken up chronologically.

Mus Linnæus, 1758 (*Syst. Nat.*, Ed. 10, p. 59), contained the following species: *Porcellus*, *leporinus*, *lemmus*, *marmota*, *monax*, *ericetus*, *terrestris*, *amphibius*, *rattus*, *musculus*, *avellanarius*, *sylvaticus*, *striatus*, *longipes*, *jaculus*, *volans*. Since two² of these (*lemmus* and *terrestris*) are

¹An account of the migrations of *Lemmus lemmus* in Norway is given by Prof. R. Collett in *Christiania Videnskabs-Selskabs Forhandling*, 1895, No. 3.

For description of a vole plague in Scotland, see Report of the Departmental Committee appointed by the Board of Agriculture to inquire into a Plague of Field Voles in Scotland. London, 1893.

²Apparently three, but *terrestris* and *amphibius* are, as Lataste has already shown, the same animal. The *Mus amphibius* of Linnæus is nothing more than a figment of the imagination based on Ray's misconception that there is a large aquatic vole with webbed feet.

Since the matter is of importance as determining the validity of the current name of one of the most common European mammals, I quote Linnæus's descriptions in full:

"[*Mus*] *terrestris*, 7. *M. cauda mediocri subpilosa, palmis subtetradactylis, plantis pentadactylis, auriculis vellere brevioribus*.

"*Mus cauda longissima pilosa, auribus subrotundis vellere brevioribus*. Fn. svec. 29. *Syst. Nat.*, 10, n. 5.

"*Mus agrestis, capite grandi, brachiuros*. Raj. quadr. 218.

"*Habitat in Europæ terra et aqua*.

"*Corpus fuscum subtus pallidum, at non albicans. Caput crassius, ore gibbo. Cauda magis pilosa, quam in Ratto, sed corpore dimidio brevior, a pedibus fere longior*.

"*Hortos Talpæ instar misere effodit palmis licet parvis; natat in fossis et urinatur plantis licet fissis; Radices arborum decorticat, plantarum consumit s. aufert; Pullos anatum in piscinis occidit*.

"[*Mus*] *amphibius*, 8. *M. cauda elongata pilosa, plantis palmatis*.

"*Mus major aquaticus s. Rattus aquaticus*. Raj. quadr. 217.

"*Mus aquaticus*. Beil. aquat. 35. t. 36.

Microtines, it is necessary to see whether the name can be applied to any genus of the subfamily. Linnaeus of course designated no type, but subsequent usage has fixed the name on the congeners of *Mus musculus*. As no sound principle of nomenclature is thus violated, the name *Mus* should be kept in its present signification.

Castor Linnaeus, 1758 (Syst. Nat., Ed. 10, p. 58), was originally proposed for the species *fiber* and *moschatus*, but in the twelfth edition of the *Systema* others were included, among them the muskrat. The name, however, could by no process of subsequent elimination be applied to the latter.

Glis Brisson, 1762 (Regn. Anim., pp. 13, 113), is clearly based on the dormice,¹ although the genus includes 'la Marmotte de Bahama,' 'la Marmotte d'Amerique,' 'la Marmotte de Pologne,' 'la Marmotte des Alpes,' and 'la Marmotte de Strassbourg,' in addition to 'le Loir,' 'le Lerot,' and 'le Croquenoix.' The name must, therefore, take the place of *Myorinus* Schreber, 1781, commonly used for the dormice.² As none of the species of Brisson's *Glis* are Microtines, the name would not be mentioned here were it not for its bearing on *Glis* Erxleben, 1777.³ (See p. 13.)

Cuniculus Brisson, 1762 (Regn. Anim., p. 13), must also be considered, because it invalidates the use of *Cuniculus* Wagler as the generic name of a lemming (see page 16).⁴ The genus contained an assemblage of forms which are now put in six genera distributed among five families. Dr. C. Hart Merriam has recently shown (Science, n. s., I, p.

[Continuation of note from page 11.]

"Habitat in Europæ, Africae fossis, ripis, piscinis, hortis.

"Species mihi non rite cognita.

"Fodit ad fossas et radices arborum, natat, urinatur, consumit radices, Hortis et satis infestus, capitur Nassis e virgulis confectis sub aqua demersis."

The description of *Mus terrestris* is extended and applies to the water rat in every particular, while the diagnosis of *M. amphibius* is very brief and contains a glaring error in the assertion that the animal has webbed feet. That the common water rat was the animal which Linnaeus had in mind when he described *Mus terrestris* is shown by the length and accuracy of the description and by his choice of the specific name (*Mus terrestris* is the Latin equivalent of the Swedish jodrätta). That he never saw '*Mus amphibius*' is clearly indicated by the statement: "Species mihi non rite cognita." It is thus evident that there is no excuse for retaining the specific name *amphibius*, even though the error through which it is now generally used has passed current for nearly a century.

¹In the *Tabula Synoptica Quadrupedum secundum Ordines Sectiones et Genera*, on pages 12 and 13, the name is introduced as follows:

Cauda longa, vestita pilis ita dispositis at caudum planum efficiant.....*Sciurus*
Cauda longa, vestita pilis ita dispositis at caudum rotundum efficiant.....*Glis*

²See Merriam, Science, n. s., I, p. 376, April 5, 1895.

³*Glis* Brisson also antedates *Glis* Storr (Prodr. Meth. Mamm. 1780, p. 39), proposed for *Mus tamaricinus*, *M. longipes*, *M. cafer*, *M. sagitta*, *M. jaculus*, *M. nitidula*, *M. avellanarius*, and *M. glis*.

⁴In the synoptic table (pp. 12, 13) the name is introduced as follows:

Cauda brevissima vel nulla:

Auriculis longis*Lepus*

Auriculis brevibus vel nullis.....*Cuniculus*

376, 1895) that by elimination *Cuniculus cauda longissima* Brisson (= *Dipus alactaga* Olivier) becomes the type. The name is thus untenable for any of the *Muride*, although *Lemmus lemmus* is one of the species included by Brisson in the genus.

Glis Erxleben, 1777 (Syst. Regn. Anim., p. 358), contained *marmota*, *monax*, *canadensis*, *tscherkessicus*, *zemmii*, *lemmus*, *migratorius*, *barabensis*, *arenarius*, *lagurus*, and *aeconomicus* [= *Mus songarus* Pall.]. Although this genus contains two lemmings, the name need not be considered, since it is preoccupied by *Glis* Brisson, 1762.

*Arctomys*¹ Schreber, 1780 (Plates to Schreber's Säugth., CCVII-CCIX, 1780), contained the following species: *marmota*, *monax*, *bobac*, *empetra*, and *citillus*. Of these the first four belong to the genus *Arctomys* as now understood, and the last to *Spermophilus*. The latter genus was defined in 1823 by F. Cuvier (Dents des Mammifères, 1823, 160-162, 255), who restricted the name *Arctomys* to the group to which it is now applied. *Arctomys* Schreber is mentioned here only on account of:

Lagomys Storr, 1780 (Prodrömus Methodi Mammalium, p. 39). Although Storr and Schreber bear the same apparent date, it appears safe to take Schreber as the earlier, since Storr alludes to the genus *Arctomys*, and refers directly to the '*Mus glareolus* Schreberi,' a species published at the same time.² Storr evidently proposed *Lagomys* merely as a substitute for *Arctomys*, a name which he considered inappropriate, because the animals to which it was applied resemble hares rather than bears.³ It is thus a synonym of *Arctomys* and requires no further consideration.⁴

Myocastor Kerr, 1792 (Animal Kingdom, I, Mamm., Syst. Cat. Nos. 458-521), included the coypu and muskrat. No type was designated, but subsequent elimination fixed the name on the coypu. (See p. 14.)

Ondatra Link, 1795, (Zool. Beyträge, Vol. I, Pt. II, p. 76), contained the same species as *Myocastor* Kerr, of which the name is thus a synonym.

Lemmus Link, 1795 (Zool. Beyträge, Vol. I, Pt. II, p. 75), has escaped the notice of recent writers. Vague references to it occur in works

¹This name is apparently antedated by *Marmota* Blumenbach ("Handb. d. Naturgesch., 1779," fide Agassiz). I have been unable to verify the reference, and do not know what species were included by Blumenbach in the genus.

²On the dates of the parts of Schreber's Säugthiere, see Sherborn, Proc. Zool. Soc., London, 1891, 587.

³"Sequuntur in eundem finem nomina specierum, laudato Pallas pariter ad mures tractarum, quae mihi genus constituerunt, *Lagomys*, nec *Arctomys* dictum, nam Lepori aptius quam Urso, comparari posse videantur. Dicendæ species nominibus Ill. Pallas æque adhibitæ, hæc sunt; *M. arenarius*, *M. songarus*, *M. furunculus*, *M. cricetus*, *M. accedula*, *M. phæus*, *M. lagurus*, *M. gregalis*, *M. socialis*, *M. æconomus*, *M. rutilus*, *M. glareolus* Schreberi, *M. monax*, *M. marmota*, *M. empetra*, *M. arctomys*, *M. citillus*, *M. lemmus*, *M. torquatus*, *M. hudsonius*, *M. talpinus*, *M. capensis*, *M. aspalax*, *M. typelus*" (sic.).

⁴*Lagomys* Storr of course antedates *Lagomys* Cuvier, 1800, the current name for the pikas.

of the early part of the present century, but of late all traces have disappeared. Lataste (Le Naturaliste, Tome II, p. 473, 1852), after a long and fruitless search, concluded that the name had probably never been published, and that the references of the older authors were merely to Link's manuscript. Mr. Oldfield Thomas has discovered Link's book and finds that the genus *Lemmus* contained the species *socialis*, *lagurus*, *lemmus*, *torquatus*, *glareolus*, and *hudsonius*,¹ representing the modern genera *Lemmus*, *Dicrostonyx*, *Microtus*, and *Erotomys*. As the name *Lemmus* has been restricted by subsequent authors to the species *lemmus* and its near allies, a group to which no other generic name has been specially applied, it must be retained in this sense.²

Microtus Schrank, 1798 (Fauna Boica, p. 72), included *M. terrestris*, *M. amphibius* (= *M. terrestris* Linn.), and *M. 'gregarius'*. The *Microtus terrestris* of Schrank is not the *Mus terrestris* of Linnaeus, but the common field mouse of Central Europe, *Microtus arvalis* (Pallas). *M. gregarius* Schrank, apparently based on one specimen from Bettbrunn, is probably a young *M. arvalis*. The third species, *M. amphibius*, is the water rat, *Microtus terrestris* (Linnaeus). Thus the genus *Microtus* originally contained two species, *arvalis* and *terrestris*. As the latter was made the type of *Arvicola* by Lacépède in 1801, *arvalis* must be taken as the type of *Microtus*.

Fiber Cuvier, described in 1798 but not named until 1800 (Tabl. Élé. de l'Hist. Nat. d. Anim, 141, 1798; Leçons d'Anat. Comp. I, Tabl. I, 1800), is the first and only generic name based exclusively on the muskrat. Cuvier, in establishing this genus, eliminated *Fiber zibethicus* from *Myocastor*, and thus fixed the latter name on *M. coypu*. (See page 13.)

Arvicola Lacépède, 1801 (Mém. de l'Inst., III., Paris, 1801, 489³), was based on *Arvicola amphibius* (= *Mus terrestris* Linn.) alone, and not on the European voles in general, as often supposed.⁴ Although the name *Arvicola* can not be used in a generic sense, it is available for the sub-genus of which *Microtus terrestris* is the type.

Hypodæus Illiger, 1811 (Prodr. Syst. Mamm. et Avium, p. 87), contained the species *lemmus*, *amphibius* (= *terrestris*), and *arvalis*, or the modern genera *Lemmus* and *Microtus*. As no type was designated, and

¹ Mr. Thomas has kindly sent me a copy of the original diagnosis. It is as follows: "Gen. 8 *Lemmus*, Lemming. Die Thiere dieses Geschlechts kommen mit den vorigen [*Mus*] sehr neberein, aber die Ohren sind viel kleiner und abgerundet, der Körper gedrungener, die Beine verhältnissmässig kürzer, der Schwanz sehr kurz. Auch weichen sie in der Lebensart von den vorigen ab. Sie nähern sich *Arctomys*. Hieher gehören: *Mus socialis*, *lagurus*, *lemmus*, *torquatus*, *glareolus*, *hudsonius*."

² See note on the names *Brachyurus*, *Myodes*, *Hypodæus*, and *Lemmus*, in Actes de la Société Scientifique du Chili, Tome V, pp. XX, XXI, 1895.

³ This is sometimes quoted: "Tableau des divisions, etc., de la class des mammifères, 1799." The paper was "In le 21 prairial an. 7," though not published until 1801.

⁴ Lacépède's description is as follows: "44 Campagnol. Deux incisives supérieures non comprimées; deux incisives inférieures tranchantes; molaires sillonnées; point d'abajoues; queue velue. Campagnol aquatique—*Arvicola amphibius*."

as both *Lemmus* and *Microtus* were included in the then undivided genus *Lemmus* Link, the name *Hypudarus* must lapse into synonymy.

Myodes Pallas, 1811 (Zoog. Rosso -As., I, p. 172), embraced ten species, now placed in four genera. The species are: *Lemmus*, *torquatus*, *lagurus*, *aeconomus*, *arvalis*, *saxatilis*, *gregalis*, *socialis*, *alliarinus*, and *rutilus*; the genera: *Lemmus* (*lemmus*), *Dicrostonyx* (*torquatus*), *Microtus* (*aeconomus*, *arvalis*, *saxatilis*, *gregalis*, *socialis*, *alliarinus*, *lagurus*), and *Erotomys* (*rutilus*). Since *Myodes* contained species of exactly the same modern genera as *Lemmus* Link and no groups not included in the latter, the name is a synonym of *Lemmus*.

Brachyurus Fischer, 1813 (Zoognosia, I, 3d ed., pp. 14, 24: III, 1814, p. 55), contained the species: *arvalis*, *rutilus*, *amphibius*, *lemmus*, *torquatus*, *alliarinus*, *blumenbachii*, *fulvus* Geoffroy, *niloticus* Geoffroy; also the 'species dubiae': *zemni*, *gregarius*, *socialis*, *lagurus*, *aeconomus*. The name is a pure synonym of *Lemmus* Link, unless it may be applied to some of the exotic or dubious species.¹

Alriccola Blainville, 1817 (Nouv. Dict. d'Hist. Nat., IX, p. 287), proposed for 'le Genre Campagnol' is probably an erratic misprint for *Arricola*. No type is mentioned.

Mynomes Rafinesque, 1817 (American Monthly Magazine, II, p. 45), was based on Wilson's figure of the common meadow mouse of the eastern United States. The name is thus a synonym of *Microtus* Schrank, as *Microtus arvalis* and *M. pennsylvanicus* can not be separated subgenerically.

Psammomys LeConte, 1830 (Ann. Lyc. Nat. Hist., N. Y., III, p. 132), is the first name proposed for the subgenus containing *Microtus pineorum*. It is, however, preoccupied by *Psammomys* Cretzschmar, 1828 (Atlas zu der Reise im Nördl. Afrika. 1ste Abth., Zool. (1826), Heft XI, 1828, p. 56. Type *Psammomys obesus* Cretzschmar) and so can not be used here. The date of *Psammomys* LeConte is usually quoted as 1829, but the paper on this genus, although read on December 21, 1829, was probably not published until after the end of January, 1830, since papers read January 11-25, 1830, are included with it in one signature.

Pitymys McMurtrie and *Ammomys* Bonaparte both appeared in 1831.

McMurtrie (American ed. Cuvier's Règne Animal, I, p. 434) pointed out that *Psammomys* LeConte is preoccupied, and for this name substituted *Pitymys*. Bonaparte (Saggio Distrib. Metod. degli Anim. Vert., p. 20, footnote) after showing that LeConte's name *Psammomys* is not tenable, proposed to change it to *Ammomys*, thus preserving the original meaning of the word.² It is impossible to tell which name is the earlier,

¹ This name has been supposed to be preoccupied by *Brachyurus* Spix (Latate, Ann. Mus. Civ. St. Nat. di Genova, XX, p. 264; Büchner, Wissensch. Result. der von N. M. Przewalski unternomm. Reisen, I, p. 127). Spix's name, however, dates from 1823 and would in no way invalidate *Brachyurus* Fischer, were the latter on other grounds tenable.

² "Prendiamo la libertà d' introdurre una piccola mutazione ortografica nel nome dato al nuovo genere dal Sig. LeConte, la quale non ne cambia però il significato."

but in the uncertainty *Pitymys* should be retained as the one adopted by all subsequent writers.

Cuniculus Wagler, 1830 (Nat. Syst. d. Amphibien, p. 31), included three species (*C. lemmus*, *C. torquatus*, and *C. aspalax*) now referred to three genera and two subfamilies. The name has been commonly applied to *torquatus* and its congeners, but its use is invalidated by *Cuniculus* Brisson, published fifty-eight years before.

Hemiotomys DeSelys-Longchamps, 1836 (Essai monograph. sur les Campagnols des environs de Liège, p. 7), was proposed as a section of *Arvicola* (= *Microtus*) to include the species *fulvus* (= *arvalis*) and *amphibius* (= *terrestris*). As each of these had already received a tenable subgeneric name, *Hemiotomys* lapses into synonymy.

Pinemys Lesson, 1836 (Hist. Nat. d. Mamm. et Ois. découv. depuis 1788, Compl. (Œuvres de Buffon, V, p. 436), based on *Psammomys pinctorum* LeConte, is a synonym of *Pitymys* McMurtrie.

Lagurus Gloger, 1841 (Gemeinnütz. Hand- u. Hilfsbuch d. Naturgeschichte, I, pp. XXXI, 97), is the earliest available name for the subgenus of which *Mus lagurus* Pallas is the type.¹ (See footnote, p. 49.)

Dicrostonyx Gloger, 1841 (l. c., pp. XXXI, 97), is the tenable name for the genus usually known as *Cuniculus* Wagler.² This name has escaped notice until very recently.³

Neodon Hodgson, 1849 (Ann. & Mag. Nat. Hist., 2d ser., III, p. 203), is a synonym of *Microtus*, as its type, *N. sikkimensis* Hodgson, can not be separated subgenerically from *Microtus arvalis*.

"*Myolemmus* Pomel, 1854 (Ann. Sci. Soc. Auvergne)," is a synonym of *Dicrostonyx* Gloger. This statement is made on the authority of Trouessart (Cat. Mamm. viv. et foss., Rodentia, Pt. II, p. 156, 1881), as I have had no opportunity to verify the reference.

Misothermus Hensel, 1855 (Zeitschr. der Deutsch. geolog. Gesellsch., VII, p. 492), is stated by the author to be based on *Myodes torquatus* Pall. It is thus antedated by *Myolemmus* Pomel and *Dicrostonyx* Gloger.

Pedomys, *Chilotus*, and *Synaptomys* are three names proposed by Baird in 1857 (Mamm. N. Am., pp. 516, 517, 558). All are tenable for the groups to which they were applied. *Pedomys* and *Chilotus* are subgenera of *Microtus*. Their types are *Microtus austerus* and *M. oregonus*, respectively. *Synaptomys* is a genus, with *S. cooperi* as the type.

¹Gloger's description is as follows: "Theils auf dem Ural und anderen Gebirgen, theils auch in tieferen Gegenden Sibiriens, giebt es, drei oder vier andere Arten mit kleinen, rundlichen oder spitzigen Daumnägeln und von einfacherer Färbung (*Lagurus*), die zum Theile nicht weniger zum Wandern geneigt scheinen. Z. B. *L. migratorius*."

²Gloger says: "Von den nordamerikanischen Lemmingen zeichnen sich manche durch ein Paar höchst sonderbare (gleichsam doppelte) Vorderkrallen aus, die 2 oder gar 3 Spitzen über einander zu haben scheinen, weil sie unter den Nägeln grosse, harte Ballenhervorragungen besitzen. Sie können daher Gabelkraller (*Dicrostonyx*) heissen."

³For a paper on Gloger's generic names for mammals, see Thomas, Ann. & Mag. Nat. Hist., 6th ser., XV, Feb. 1, 1895.

Paludicola Blasius, 1857 (Fauna der Wirbelth. Deutschl., Bd. I, Säugethiere, p. 333), a subgenus of *Arvicola* (= *Microtus*), contained the species: *amphibius* (= *terrestris*), *nivalis*, and *ratticeps*. As the first is a member of the subgenus *Arvicola* and the others each a true *Microtus*, the name can not be used. Moreover, it is preoccupied by *Paludicola* Wagler, 1830 (Nat. Syst. d. Amphibien, p. 206, type *Bufo albifrons* Spix).

Agricola Blasius, 1857 (l. c., p. 334), was proposed as a subgeneric name for *Microtus agrestis*. The differences between this species and the allies of *M. arvalis* are too slight to entitle the groups to rank as distinct subgenera; but assuming that it were desirable to separate them the name *Agricola* would be antedated by *Mynomes* Rafinesque, 1817, based on *Microtus pennsylvanicus*, a form whose superspecific characters are exactly similar to those of *M. agrestis*.

Phaiomys Blyth, 1863 (Journ. Asiat. Soc. Bengal, XXXII, p. 89), is the first and only tenable name proposed for the subgenus having *Microtus blythi* as the type.

Ochetomys Fitzinger, 1867 (Sitzungsb. K. Akad. Wiss. Wien, LVI, June, 1867, p. 47), included the water rats of Europe. It is thus equivalent to *Arvicola* Lacépède.

Praticola Fatio, 1867 (Les Campagnols du Bassin du Léman, p. 36), is a subgenus of *Arvicola* (= *Microtus*) containing: *amphibius* (= *terrestris*), *nivalis*, *arvalis*, *ratticeps*, and *campestris* (= *arvalis*?). As all of these are species either of *Microtus* Schrank, or *Arvicola* Lacépède, the name *Praticola* can not stand. *Praticola* is, moreover, preoccupied in ornithology.

Sylricola Fatio, 1867 (l. c., p. 63), based on *Microtus agrestis* is exactly equivalent to *Agricola* Blasius, 1857. The name is preoccupied in ornithology, entomology, and conchology.

Terricola Fatio, 1867 (l. c., p. 73), contained *Microtus subterraneus* and *M. sarii*. The name is, however, preoccupied in conchology by *Terricola* Fleming, 1828.

Isodelta and *Anaptogonia* Cope, 1873 (Proc. Am. Philos. Soc., XII, p. 87), are the tenable names for two extinct subgenera found in the Post-pliocene cave deposits of Pennsylvania. Their types are *Microtus speothen* and *M. hiatidens*, respectively.

Erotomys Coues, 1874 (Proc. Acad. Nat. Sci. Phila., p. 186), is the tenable name for the genus of which *Mus rutilus* is the type.

Micrurus Forsyth Major, 1876 (Atti della Società Toscana di Sci. Naturali, III, fasc. I, p. 126), founded on Mina Palumbo's description of *Arvicola nebrodensis* (a *Pitymys*), is preoccupied by *Micrura* Ehrenberg, 1831, a genus of Vermes.

Alticola Blanford, 1881 (Journ. Asiat. Soc. Bengal, L, pt. 2, p. 93), is the only name proposed for the Asiatic subgenus with *Microtus stoliczkanus* as type.

Eremiomys and *Borioikon* Polyakoff, 1881 (Mém. Acad. Imp. Sci. St.

Petersbourg, XXXIX suppl., p. 34), based, respectively, on *Mus lagurus* Pallas and *Mus torquatus* Pallas, are synonyms of *Lagurus* Gloger and *Dicrostonyx* Gloger.

Neofiber True, 1884 (Science, IV, p. 34), was described as a genus with *N. alleni*, the only known species, as type. Recently it has been shown that the characters of the animal are not enough to separate it generically from *Microtus*, of which, however, *Neofiber* forms a well-marked subgenus.¹

Lasiopodomys Lataste, 1887 (Annali del Mus. Civ. di Storia Naturale di Genova, ser. 2a, Vol. IV, p. 268), is a synonym of *Phaiomys* Blyth, 1863, the species on which the two names were based, *Microtus brandti* Radde and *Microtus blythi* Blanford (= *M. leucurus* Blyth nec *Arvicola leucurus* Gerbe), respectively, being in no way separable subgenerically.²

Phenacomys Merriam, 1889 (North Am. Fauna, No. 2, p. 28), is the tenable name for the genus of which *Phenacomys intermedius* is the type.

Campicola Schulze, 1890 (Schriften Naturwiss. Vereins d. Harzes in Wernigerode, V, p. 24), is a subgenus formed for the reception of the species *Microtus arvalis*, *M. subterraneus*, and *M. campestris*. It is thus a compound of two subgenera, *Microtus* (*arvalis* and *campestris*) and *Pitymys* (*subterraneus*), each of which has previously received a tenable name. *Campicola* is, moreover, preoccupied in ornithology (Swainson, 1827).

Bramus Pomel, 1892 (Comptes Rendus, Paris, CXIV, p. 1159), is based on a mandible and the teeth of both jaws of a rodent from the Quaternary phosphorites of Trara de Nédroma near Ain-Mefta, Tunis. Although the author compares this fossil with the bones and teeth of the water rat, he points out such striking differences between the two that it is very doubtful whether *Bramus* can be considered a member of the subfamily *Microtine*. (See p. 73.)

Aulacomys Rhoads, 1894 (American Naturalist, XXVIII, p. 182), although based on an abnormal specimen, is the tenable name for a group of American water rats, should the latter be considered subgenerically distinct from *Arvicola*. The peculiarities of the original specimen of *Microtus arvicoloides*, the type of *Aulacomys*, are such that the group was originally given full generic rank.

Mictomys True, 1894 (Proc. U. S. Nat. Museum, XVII, No. 999, p. 242, Advance Sheet, April 26), was proposed as a full genus with *Mictomys innuitus* True for the type and only known species. The name is tenable, but the group is only a subgenus of *Synaptomys*.³

Tetramerodon Rhoads, 1894 (Proc. Acad. Nat. Sci. Phila., p. 282), is the most recent synonym of *Microtus*. The author, as Blasius had

¹True, Report of the Smithsonian Institution for 1884, Part II, pp. 325-330, Pl. II. Merriam, North American Fauna, No. 5, p. 60, 1890. Chapman, Bull. Am. Mus. Nat. Hist., New York, VI, p. 334, 1894.

²See Actes de la Société Scientifique du Chili, IV, p. CLXXXVIII, 1894.

³See Merriam, Proc. Biol. Soc. Washington, X, p. 57, 1896.

already done nearly forty years before, divides the subgenus *Arvicola* (= *Microtus*) into two groups, based on the structure of the middle upper molar. To the species with this tooth formed of five prisms he restricts the name *Myonomes*, while to those with the same tooth made up of only four prisms he applies the new name *Tetramicrodon*. The character in question is far too trivial to serve alone as the basis for a subgenus. If, however, the advisability of subdividing the genus along such narrow lines be admitted, the name *Tetramicrodon* still becomes a synonym of *Microtus*, since *M. arvalis*, the type of the latter, is itself a species with the middle upper molar four parted.

HISTORY OF FORMER CLASSIFICATIONS.

The most important studies of the various groups of *Microtinae*, but more especially of the subgenera of *Microtus*, are those of De Selys Longchamps (1836 to 1862), Blasius (1857), Baird (1857), Fatio (1867), Coues (1874), Blanford (1881), and Lataste (1887). The names used by these authors for the subdivisions of *Microtus* adopted in the present classification are shown in the accompanying table:

Table of Names used by Authors for the Subgenera of *Microtus*.

Names used in the present paper.	De Selys Longchamps, 1836 to 1862.	Blasius, 1857.	Baird, 1857.	Fatio, 1867.	Coues, 1874.	Blanford, 1881.	Lataste, 1887.
<i>Arvicola</i>	<i>Hemiotomys</i>	<i>Paludicola</i>	<i>Praticola</i> (part).	<i>Arvicola</i> .
<i>Microtus</i>	<i>Arvicola</i> ..	<i>Arvicola</i> (part).	<i>Praticola</i> (part).
	<i>Myonomes</i> ..	<i>Agricola</i> ..	<i>Hemiotomys</i> .	<i>Sylvicola</i> ..	<i>Myonomes</i>	<i>Neodon</i> , (part).	<i>Microtus</i> .
<i>Pitymys</i>	<i>Microtus</i>	<i>Arvicola</i> (part).	<i>Pitymys</i> ..	<i>Terricola</i> ..	<i>Pitymys</i>	<i>Pitymys</i> .
<i>Pedomys</i>	<i>Pedomys</i>	<i>Pedomys</i>
<i>Phaiomys</i>	<i>Paludicola</i>	<i>Lasiopodomys</i> .
<i>Chilotus</i>	<i>Chilotus</i>	<i>Chilotus</i>
<i>Lagurus</i>
<i>Alticola</i>	<i>Alticola</i>
<i>Hyperacrius</i>	<i>Alticola</i> part ?.
<i>Eothenomys</i>	<i>Neodon</i> (part).
<i>Antelomys</i>
<i>Neofiber</i>

De Selys Longchamps published two extended papers on the European *Microtinae*, and later a note supplementary to the first of these. The first paper appeared in 1836 under the title 'Essai Monographique sur les Campagnols des environs de Liège.' In this the author showed that hitherto the voles had been divided into two groups, according to their habits, the aquatic species being separated from those that are

strictly terrestrial. This proved unsatisfactory because the two were found to intergrade imperceptibly. Hence he proposed to rearrange the species according to the length of the ears. The first division, or that in which the ears are extremely short or apparently absent, he named *Hemiotomys*. This the author subdivided into two sections, neither of which he named. The first contained one species, *Arvicola fulvus* (= *Microtus arvalis*), distinguished by its short tail and by the supposed absence of external ears. The second contained the water rat. To *Arvicola* (= *Microtus*) proper were referred the three species, *arvalis*, *subterraneus*, and *rufescens* (= *Erotomys glareolus*). Six years later, in his *Études de Micromammalogie*, De Selys Longchamps followed the same system of classification, but considerably extended it and included species from Asia and North America. This later scheme is as follows:

The genus is first divided into two sections, one of which consists of species with ears shorter than the fur and with very small eyes, the other of species with the ears as long as the fur and with the eyes well developed. The first section contains two groups, (1) *Hemiotomys* with the European water rats and the American *Arvicola riparius* (= *Microtus pennsylvanicus*), and (2) *Microtus* with the species *fulvus*, *savii*, *æconomus*, and certain American forms not mentioned by name. The second section is divided into three groups: (1) *Arvicola* with the species *subterraneus*, *arvalis*, *gregalis*, *alliarius*, *duodecimcostatus*, and *socialis*; (2) *Myodes* with the two species *rubidus* (= *Erotomys glareolus*) and *rutilus* (= *Erotomys rutilus*); (3) *Mynomes* with the species *pratensis* (= *Microtus pennsylvanicus*). These groups and sections the author considers in no way entitled to rank as genera or subgenera. He names them merely for convenience.¹ In a postscript published at the time of distribution of the last copies of the *Essai Monographique*, twenty-six years after its appearance, the author makes a few corrections in the classification previously adopted. He points out that his *Arvicola fulvus* is merely a young specimen of *A. arvalis* that by accident had lost its external ears. and, furthermore, that the species *subterraneus* should be transferred to the section *Microtus*.

The classification as finally perfected is as follows:

Genus *Arvicola*:

Group *Hemiotomys* (water rats).

Group *Microtus* (*subterraneus* and *savii*).

Group *Arvicola* (typical voles).

Group *Myodes* (*glareolus*).

Group *Mynomes* (*pennsylvanicus*).

¹ Je dois prévenir que je m'opposerais entièrement à l'élévation d'aucune de ces sections au rang de genre ou de sous-genre. Toutes passent de l'une à l'autre par des nuances insensibles dans la longueur de la queue et des oreilles; et, quant au caractère tiré de la racine des dents, il est probable qu'il existe à un degré plus ou moins fort chez d'autres espèces. Si je me suis permis d'imposer à ces groupes des noms latins pris parmi les synonymes du genre, ce n'est nullement pour qu'ils puissent être introduits dans la nomenclature binaire, mais pour donner aux étrangers l'idée des divers noms que j'ai employés en français. (*Micromammalogie*, p. 87.)

The groups *Hemiotomys*, *Microtus*, and *Arvicola* of De Sélvs Longchamps are exactly equivalent respectively to the subgenera *Arvicola*, *Pitymys*, and *Microtus* of the present paper, while *Myodes* is the same as the genus *Erotomys*. The group *Mynomes* based on Rafinesque's description of *Mynomes pratensis* (= *Microtus pennsylvanicus*) should be united with *Arvicola* (*Microtus*, as now understood), a course which the author no doubt would have followed had he been acquainted with the type species.

Blasius published in 1857, in his 'Fanna der Wirbelthiere Deutschlands,' a classification of the voles based primarily on the pattern of enamel folding in the first and second molars of the lower jaw and the second molar of the upper jaw. This system differs in many ways from that of De Sélvs Longchamps, and is as follows:

Genus *Arvicola*:

Subgenus *Hypudaus* (*glarcolus*).

Subgenus *Paludicola* (*amphibius* [= *terrestris*], *nivalis*, *ratticeps*)

Subgenus *Agricola* (*agrestis*).

Subgenus *Arvicola*:

A. *Arvicola* (*campestris*, *arvalis*).

B. *Microtus* De Sélvs part (*subterraneus*, *savii*).

The subgenus *Arvicola* Blasius subdivides into two sections, A. *Arvicola* and B. *Microtus* De Sélvs (part). The former includes the species *campestris* and *arvalis*, the latter *subterraneus* and *savii*. The subgenus *Hypudaus* and the section *Microtus* are equivalent, respectively, to the genus *Erotomys* and the subgenus *Pitymys* of the present paper. Of the other groups, the restricted *Arvicola* contains the typical species of the subgenus *Microtus*, *Agricola*, a slightly aberrant form of the same, and *Paludicola*, the subgenus *Arvicola* and two aberrant members of the subgenus *Microtus*. Blasius's subgenera *Paludicola* and *Arvicola* are excellent illustrations of the unnatural results of a system of classification based on one set of characters. While there is a general similarity between the enamel pattern of the three species associated in the former, *Microtus terrestris* differs from *M. ratticeps* and *M. nivalis* in the form of the skull, the number of plantar tubercles, the quality of the fur, and in the presence of large musk glands on the sides. In the subgenus *Arvicola* Blasius associates two of the most distinct subgenera of the genus *Microtus* (*Microtus* and *Pitymys*), and treats the differences in the number of mammae and footpads, form of skull, and size of eyes as matters of trifling importance in comparison with the general similarity of the enamel pattern. On the other hand, the author recognizes *Agricola* as a full subgenus, when the chief character on which the group is based is the presence of a minute supplemental postero-internal prism on the middle upper molar.

The classification adopted by Baird (Mamm. N. Am., 1857) is based on a combination of characters, and is thus much more satisfactory than the artificial arrangement published almost simultaneously by

Blasius. His classification of the subdivisions of *Microtus* is as follows:

Genus *Arvicola*:

Subgenus *Hypudæus* (*gapperi*).

Subgenus *Arvicola* (typical voles).

Section *Hemiotomys* (most of the American species and the European *agrestis*).

Section *Chilotus* (*oregoni*).

Section *Pedomys* (*austerus*).

Section *Pitymys* (*pinctorum*).

Baird's subgenera *Hypudæus* and *Arvicola* are equivalent to the genera *Erotomys* and *Microtus* of the present paper, while his sections *Chilotus*, *Pedomys*, and *Pitymys* are equal to the subgenera of the same names. The section *Hemiotomys* of Baird is the *Arvicola* of De Selys Longchamps, and the subgenus *Microtus* of the present paper.

In 1867 Fatio published a classification of the European voles in a paper entitled 'Les Campagnols du Bassin du Léman.' This arrangement is essentially the same as that of Blasius. Fatio, however, recognizes *Hypudæus* (= *Erotomys*) as a full genus, and raises the second of Blasius's two sections of the subgenus *Arvicola* to the rank of a subgenus, while the first he unites with *Microtus terrestris*, *M. nivalis*, and *M. ratticeps* to form the subgenus *Praticola*. He also arbitrarily changes the names of certain groups. His classification is as follows:

Genus *Hypudæus* (*glareolus*).

Genus *Arvicola*.

Subgenus *Praticola* ('*amphibius*,' *nivalis*, *arvalis*, *ratticeps*, *campestris*).

Subgenus *Sylvicola* (*agrestis*).

Subgenus *Terricola* (*subterraneus*, *savii*).

The subgenus *Terricola* and the genus *Hypudæus* are equal, respectively, to the subgenus *Pitymys* and the genus *Erotomys* of the present paper. The subgenus *Sylvicola* is equivalent to the subgenus *Agricola* of Blasius, like it containing the pentamerodont species of the subgenus *Microtus*. The subgenus *Praticola* includes the type species of both *Arvicola* and *Microtus*, together with three other tetramerodont species of the latter.

In 1874 Dr. Coes published, in the Proceedings of the Academy of Natural Sciences of Philadelphia, an abstract of his monograph of the North American Muridæ, which appeared in full in Volume XI of the Report of the United States Geological Survey of the Territories (Monographs of North American Rodentia). Here he presented a classification of the American *Microtineæ* based primarily on Baird's review of the group. The differences between the arrangements adopted by Baird and Coes are so slight that a few words only are necessary in regard to the latter. Dr. Coes recognizes the red-backed mice as a distinct genus, which he calls *Erotomys*, after showing that the name *Hypudæus* generally used for the group is untenable. The subgenera of *Microtus* adopted by Dr. Coes are exactly equivalent to Baird's

sections of his typical subgenus *Arricola*. Dr. Coues points out Baird's error in the application of the name *Hemiotomys* De Selys Longchamps, and substitutes for the latter the equally untenable *Mynomes* Rafinesque.

In 1881 Blanford proposed, in the Journal of the Asiatic Society of Bengal (Vol. L, Pt. II, pp. 88-117), a classification of the voles of the Himalayas, Tibet, and Afghanistan. The species occurring in this region he arranges in three sections, thus:¹

Genus *Arricola*:

Section *Paludicola*, (*blythi*, *mandrianus*).

Section *Alticola* (*stoliczkaus*, *stracheyi*, *roylei*, *blanfordi*, *wyunei*).

Section *Neodon* (*sikkimensis*, *melanogaster*).

Blanford's 'sections' *Paludicola* and *Neodon* are excellent instances of unnatural classifications based on single characters. *Microtus blythi* and *M. mandrianus* are species of *Phaiomys*, a subgenus which differs from the water rats or from *Microtus* (*Microtus*) *nivalis* and *M. (M.) rattiiceps* (all of which were included by Blasius in *Paludicola*) in many important characters. Because there is a general likeness in the pattern of enamel folding they are united under one superspecific name. Again, Blanford places in the section *Neodon* the species *Microtus sikkimensis*, which is a slightly abnormal member of the subgenus *Microtus*, and *Microtus melanogaster*, a species with the bony palate formed exactly as in the red-backed mice (*Erotomys*). These members of widely different groups are brought together on account of a very superficial likeness in enamel pattern. Blanford's section *Alticola* is probably equal to the subgenera *Alticola* and *Hyperacrius* of the present paper, though it is still a matter of doubt whether it actually included any members of the latter.

The most recent classification of the subgenera of *Microtus* is that proposed by Lataste. This author has published two important papers on the subject, the first in Le Naturaliste (Tome II, pp. 323, 324, 332-334, 342, 343, 347-349, 1883), and the second in the Annali del Museo Civico di Storia Naturale di Genova (Serie 2a, Vol. IV, pp. 259-274, 1887). While recognizing the unsatisfactory nature of the artificial classification adopted by Blasius, Lataste subdivides the voles in accordance with a system fully as arbitrary as that followed by any of his predecessors. According to Lataste the characters derived from the teeth of the voles are of no value except in distinguishing between genera.² The subgenera he arranges according to the number of man-

¹ Blanford adopted Blasius's classification of the voles at large (pp. 91, 92). Except in the case of *Paludicola*, however, he supposed that none of the European sections of the genus *Microtus* are represented in the region with which he deals.

² "Chez les Rongeurs du moins, sinon chez tous les Mammifères, les caractères de la denture me semblent d'ordre générique quand ils sont suffisamment nets et tranchés, mais sans aucune importance taxonomique quand ils sont aussi minimes que ceux que l'on invoque d'ordinaire, à la suite de Blasius, chez les Campagnols, et

mæ and plantar tubercles. Although this system leads to a tolerably satisfactory arrangement of the European voles, it can not be applied to the genus at large, since it would unite such distinct groups as *Arvicola* and *Chilotus*, or *Neofiber* and *Pitymys*. Lataste's classification is as follows:

Genus *Microtus*:

Subgenus *Myodes* (*rutilus*, *glareolus*).

Subgenus *Microtus* (*gregalis*, *orrallis*, *agrestis*, *ratticeps*, *pennsylvanicus*, *nirois*).

Subgenus *Arvicola* (*terrestris*, *unsignani*).

Subgenus *Pitymys* (*pinetorum*, *subterraneus*, *socialis*, *middendorffi*).

Subgenus *Lasiopodomys* (*brandti*).

The subgenera *Myodes* and *Lasiopodomys* are equal, respectively, to the genus *Erotomys* and the subgenus *Phaiomys* of the present paper. The subgenera *Microtus* and *Arvicola* coincide with groups here recognized under the same names, while the subgenus *Pitymys* is essentially the same as that defined on page 58. Lataste, however, includes in *Pitymys* the species *middendorffi*, which is probably not a member of that group as now understood.

CHARACTERS ON WHICH THE PRESENT CLASSIFICATION OF THE
SUBGENERA OF MICROTUS IS BASED.

In the discussion of the systems of classification hitherto adopted, the impracticability of subdividing the genus *Microtus* according to the variations in any one set of characters has been shown. The highly artificial systems of Blasius and Lataste give the best examples of the unnatural results to which any such course must inevitably lead. In the present paper the classification used is based on an assemblage of characters. The more important of these, or the ones least adapted to the special needs of the different animals, and hence least likely to vary, are: Form of skull, structure of bony palate, pattern of enamel folding, number of mammæ, number of plantar tubercles, and presence or absence of musk glands on the sides. Characters of less importance, because more readily modified to fit a species to the special requirements of its environment, and hence more unstable, are: Quality of fur, hairiness of soles, length of tail, form of front feet, size of eyes, and form of external ear. It is only through careful consideration of all these that a satisfactory arrangement of the species can be obtained.

Nearly all of the characters now used have been recognized in classifications already proposed. In every case, however, they have been assigned degrees of importance different from those which they now receive. To take the three most conspicuous examples: De Selys Longchamps arranged the voles with regard to their external form;

qui portent sur les extrémités mal définies et éminemment variables, soit postérieur de la dernière molaire supérieure, soit antérieur de la première molaire inférieure." (Ann. del Mus. Civ. di Genova, Ser. 2a, Vol. IV, p. 260 footnote.)

Compare with this the opinion expressed by Büchner. (See footnote, p. 25.)

To Lataste is due the credit of recognizing the true status of the name *Microtus*.

Blasius based his classification on the pattern of enamel folding without regard to external characters, and Lataste subdivided the group according to the numbers of mamme and plantar tubercles, disregarding everything else. The impossibility of reaching satisfactory results by any of these methods has been pointed out by Büchner, who, however, takes an equally extreme position in his reluctance in any way to subdivide the genus *Microtus*.

Büchner was first to recognize the important fact that the enamel pattern, while variable within certain limits and hence of little value taken by itself, is nevertheless of considerable systematic importance when considered in connection with other characters.¹

In about 75 per cent of the specimens of a given species the enamel pattern conforms to a type which may be considered normal.² Among the abnormal specimens constituting the remainder, the variation, however, is very considerable. In the accompanying illustrations (figs. 1, 2, 3, 4, 5, and 6) are shown some of the conspicuous aberrations in the form of the teeth of *Microtus pennsylvanicus*.³ In the descriptions which follow the normal enamel pattern is alone considered.

¹After mentioning Lataste's view (see footnote, p. 23), Büchner says: "Meiner Ansicht nach liefert im Gegentheil der Bau der Backenzähne, obwohl derselbe zuweilen auch im Bereiche einer Art leicht variirt, ein vorzügliches Merkmal, welches allein genommen für die Charakteristik einer Art nicht genügt, in Verbindung aber mit den übrigen Merkmalen sehr grosse Dienste leistet und von bedeutendem systematischen Werthe ist." (Wissenschaftliche Resultate der von N. M. Przewalski nach Central-Asien unternommenen Reisen. Zool. Theil, Bd. I, Säugethiere, Lief. 3, 1889, p. 97.)

²Among 285 specimens of *Microtus pennsylvanicus* 71, or 24.9 per cent have the enamel pattern in some way abnormal. Of these, 26, or 9.1 per cent, have the first outer triangle in m 3 communicating more or less freely with the inner triangle (fig. 3); one has the second outer triangle opening into the posterior loop (fig. 3); two have the posterior loop of very unusual shape (fig. 3); one has a second inner closed triangle in m 3 (fig. 3), and 14, or 4.9 per cent, show a distinct fourth salient angle on the outer side of the same tooth. In the first lower molar 24, or 8.3 per cent, have 6 closed triangles (fig. 4), one has only 3, still another has 7 (fig. 4), while in 5, or 1.7 per cent, there are 4 (fig. 4). Of these 285 specimens m 3 is abnormal in 44 cases, or 15.4 per cent, m 1 in 31 cases, or 10.8 per cent. Grouping the abnormalities according to their frequency, they may be arranged as follows:

m 3 has first outer triangle open in 26 cases, or 9.1 per cent.

m 1 has one additional triangle in 24 cases, or 8.3 per cent.

m 3 has an additional salient angle on the outer side in 14 cases, or 4 per cent.

m 1 has one less triangle than usual in 5 cases, or 1.7 per cent.

m 3 has the posterior loop of very unusual shape in 2 cases, or 0.7 per cent.

m 3 has the second outer triangle abnormal in 1 case, or 0.35 per cent.

m 3 has an additional inner triangle in 1 case, or 0.35 per cent.

m 1 has two additional closed triangles in 1 case, or 0.35 per cent.

m 1 has two less closed triangles than usual in 1 case, or 0.35 per cent.

³The drawings here reproduced are all from specimens taken in the eastern and central parts of the United States and adjoining British Provinces. They are selected from the series of about 170 belonging to the United States Department of Agriculture.

The value of the structure of the bony palate as a taxonomic character was first pointed out by Cones,¹ who, however, considered it of rather more importance than it really is. It was at first supposed that the bony palate of all the members of the genus *Microtus* differed in a constant way from those of *Erotomys*. Mr. Oldfield Thomas has, however, recently described a *Microtus* (*M. chinensis*) in which the palate structure of *Erotomys* is almost exactly reproduced; and on further

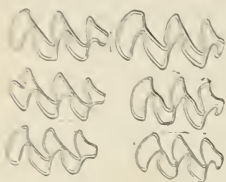


FIG. 1.—First upper molar in six specimens of *Microtus pennsylvanicus*.



FIG. 2.—Second upper molar in six specimens of *Microtus pennsylvanicus*.

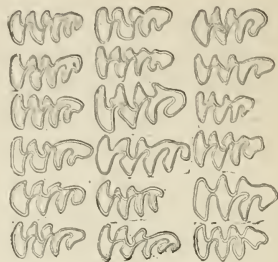


FIG. 3.—Third upper molar in eighteen specimens of *Microtus pennsylvanicus*.

study it appears that several well-marked types may be recognized among the species of the genus. These forms of palate furnish characters of considerable worth in defining many subgenera. In all, several structures remain sufficiently constant to serve as convenient landmarks. The anterior portion of the bony palate, or that formed

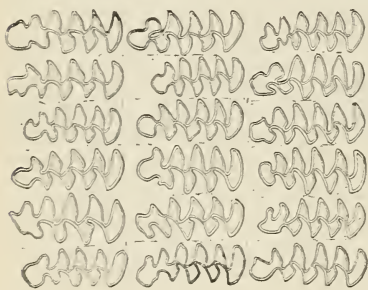


FIG. 4.—First lower molar in eighteen specimens of *Microtus pennsylvanicus*.

exclusively by the premaxillaries and maxillaries, has no special interest, as it shows very trifling variations. All the characters of importance are derived from the part lying behind the maxillo-palatine suture. This suture in the typical palate, or that occurring



FIG. 5.—Second lower molar in four specimens of *Microtus pennsylvanicus*.



FIG. 6.—Third lower molar in four specimens of *Microtus pennsylvanicus*.

in true *Microtus* and in the great majority of species and subgenera (fig. 7 A) forms a broad, U-shaped loop, the convexity of which is directed forward and whose apex lies about opposite the middle of the second molar. From this point the suture on each side sweeps rapidly backward and outward until, at the level of the anterior edge of the posterior molar, practically the whole width of the palate is occupied by the palatine, and the maxillaries are reduced to a narrow rim around the edges of the alveoli.

Until just before acquiring its greatest width, the surface of the palatine is on the same level with the rest of the bony palate, but immediately on reaching this point it changes abruptly at the sides, more gradually in the median line, to the level of the anterior border of the interpterygoid fossa, which lies about 0.5 mm. dorsad of the main part of the bony palate. In the median line the palatine slopes gently dorsocaudad to the edge of the interpterygoid fossa, a distance usually of about 1 mm., but at the sides it breaks away suddenly, and the spaces between the median sloping ridge and maxillaries are occupied by conspicuous pits (fig. 7 A, *l. p.*). The floor of each pit is continuous with the backward projection of the palatine, which runs out to join the

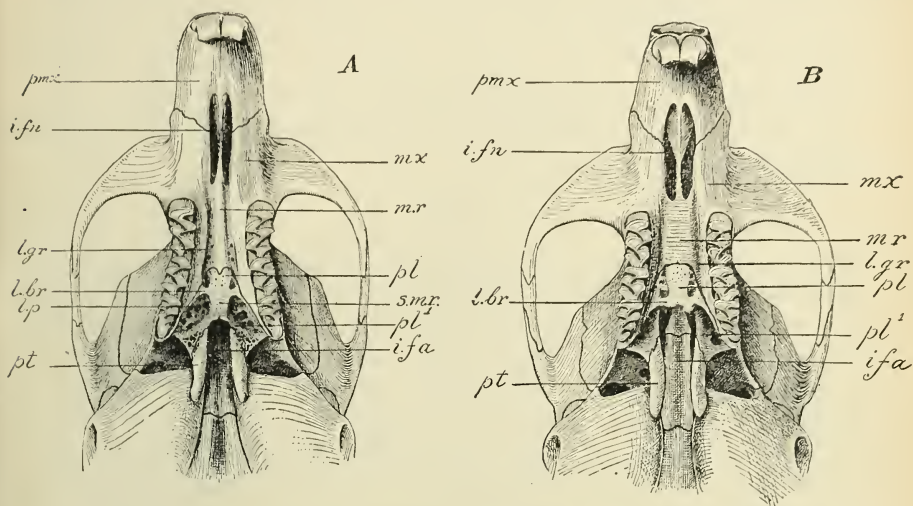


FIG. 7.—Palatal view of skull of *Microtus* (*Microtus*) *arvalis* (A) and *Erotomys* *gapperi* (B). (x 3). *i.fu.*, interpterygoid fossa (reference line crosses pterygoid fossa); *i.fu.*, incisive foramen; *l.br.*, lateral bridge; *l.gr.*, lateral groove; *l.p.*, lateral pit; *m.r.*, median ridge; *mx.*, maxillary; *pl.*, *pl'*, palatine; *pmx.*, premaxillary; *pt.*, pterygoid (reference line crosses pterygoid fossa); *s.m.r.*, sloping portion of median ridge.

pterygoid of its side (fig. 7 A, *pt.*). The ventral outline of the interpterygoid fossa (fig. 7 A, *i.fu.*) forms three sides of a figure, which is nearly a parallelogram, open at one end, the longer axis parallel with the main axis of the skull, and the length more than double the width. In front and for a short distance at the sides the fossa is limited by the palatines (fig. 7 A, *pl'*), but the greater part of its boundary is formed by the pterygoids (fig. 7 A, *pt.*). The open end lies between the hamular processes of the pterygoids. Extending back from the incisive foramina are two distinct lateral grooves (fig. 7 A, *l.gr.*), which traverse the bony palate longitudinally, leaving between them a ridge which posteriorly is continuous with the sloping median ridge already described. In these grooves open numerous foramina, larger and more crowded just in front of the region from which the bony palate slopes away to

the level of the pterygoids. The median ridge just here widens abruptly and sends out on each side a short process, which is met by a similar one arising from the palatine on the opposite side of the groove (fig. 7 A, *l. br.*). These processes usually meet and fuse, thus completely obliterating the groove, though they are frequently separated by a narrow space. In *Erotomys* (fig. 7 B) the sloping part of the median ridge has disappeared, together with the lateral pits, but traces of the median ridge (fig. 7 B, *m. r.*), the lateral grooves (fig. 7 B, *l. gr.*), and the bridges (fig. 7 B, *l. br.*) may still be recognized.

At different times subgeneric weight has been given to the form of the external ear, and to the proportional length of the tail to the head and body. Neither one, however, is of any value, except in special, isolated cases. The form of the ear is essentially the same in all the subgenera, though there are slight modifications in length and in the development of the valvular fold by which the meatus is closed.

The relative length of the tail is far too variable to serve as a useful diagnostic character.

KEYS.

The following keys to the genera and subgenera of *Microtinae* are wholly artificial and do not bring the groups together according to natural affinities. Since analytical keys are of no value except as aids in identifying specimens, it is necessary that they should be based on characters that may be studied without difficulty in ordinary museum material. Such material, however, is usually so imperfect that a single key made with reference to one set of characters (as, for instance, the form of the bony palate or the number of mammæ) might be of little use. Hence several keys are here introduced, each based primarily on a special set of structures. Of the three keys to the genera, No. 1 is made, so far as possible, with reference to the skull alone; No. 2, with reference to the teeth, and No. 3, with reference to external characters. Of the keys to the subgenera of *Microtus*, No. 5 is based primarily on characters derived from the structure of the bony palate, and is thus useless for the identification of specimens the skulls of which are not available for study. Key No. 6 is based on the pattern of enamel folding and may be used with specimens having broken skulls. The lines in italics inserted in parentheses in this key are for the identification of individuals with abnormal enamel patterns. These usually occur in the proportion of about one to four (see p. 25). Hence, one-fourth of any given lot of specimens will agree with the characters given in parentheses; the great majority, however, with those in heavy type. Key No. 7, based primarily on the mammæ and footpads, is made almost exclusively with reference to external characters. It is necessarily incomplete, since the number of mammæ and footpads is in several instances unknown. It is, of course, impossible to use this key except with alcoholic specimens or freshly killed animals. Key No. 8—if it

may be called a key—is a rough grouping of the subgenera of *Microtus* according to the essential characters used in the classification here adopted. The keys are in all cases based on the characters of adults only.

1. KEY TO THE GENERA OF MICROTINÆ.

[Based primarily on the skull.]

Skull of adult more than 50 mm. long *Fiber*
 Skull of adult less than 45 mm. long.

Molars rooted; skull always less than 30 mm. long.

Posterior border of palate a thin-edged shelf, continuous between
 alveoli of posterior molars *Erotomys*

Posterior border of palate not forming a shelf *Phenacomys*

Molars rootless; skull often more than 30 mm. long.

Middle part of zygoma expanded so as to form an oblique
 plate about 4 mm. broad *Lemmus*

Middle part of zygoma only slightly expanded.

Rostrum about $\frac{1}{2}$ total length of skull *Synaptomys*

Rostrum more than $\frac{1}{2}$ total length of skull.

Postorbital process of squamosal peg-like *Dicrostonyx*

Postorbital process of squamosal shelf-like *Microtus*

2. KEY TO THE GENERA OF MICROTINÆ.

[Based primarily on the teeth.]

Length of maxillary tooth row in adult more than 14 mm. *Fiber*

Length of maxillary tooth row in adult less than 13 mm.

Roots of lower incisors or inner (lingual) side of molar roots.

Upper incisors grooved *Synaptomys*

Upper incisors not grooved.

m 1 with 3 closed triangles *Lemmus*

m 1 with 7 closed triangles *Dicrostonyx*

Roots of lower incisors on outer side of molar roots.

Molars rooted.

Teeth weak; triangles tending to remain open; salient angles

rounded *Erotomys*

Teeth strong; triangles closed; salient angles sharp *Phenacomys*

Molars rootless *Microtus*

3. KEY TO THE GENERA OF MICROTINÆ.

[Based primarily on external characters.]

Tail flattened laterally *Fiber*

Tail terete.

Tail shorter than hind foot.

Thumb with strap-shaped nail *Lemmus*

Thumb without strap-shaped nail.

External ear rudimentary *Dicrostonyx*

External ear well developed *Microtus* (Asiatic species
 of subgenus *Lagurus*)

Tail longer than hind foot.

Upper incisors grooved *Synaptomys*

Upper incisors not grooved.

Color usually reddish; molars weak, with triangles tending

to remain open and with salient angles rounded *Erotomys*

Color brownish, grayish, or yellowish; very seldom reddish;

molars strong, with closed triangles and sharp salient angles.

Molars rooted *Phenacomys*

Molars rootless *Microtus*

4. KEY TO SUBGENERA OF SYNAPTOMYS.

- Mandibular molars with closed triangles on outer side. *Synaptomys*
 Mandibular molars without closed triangles on outer side. *Mictomys*

5. KEY TO THE SUBGENERA OF MICROTUS.

[Based primarily on the bony palate.]

- Palate normal or nearly so (see p. 27).
 Third lower molar with all triangles closed. *Lagurus*
 Third lower molar normally without closed triangles.
 Claws small, those on front feet always shortest.
 Plantar tubercles 6. *Microtus*
 Plantar tubercles 5.
 Tail more than 30 per cent of total length. *Arvicola*
 Tail less than 30 per cent of total length.
 m 1 with 5 closed triangles. *Chilotus*
 m 1 with 3 closed triangles. *Pedomys*
 Claws large, those on front feet usually longest.
 Fur long and soft. *Phaiomys*
 Fur dense and mole-like. *Pitymys*
 Palate highly abnormal.
 Palate ending in a broad median plate cut off from maxillaries at the sides.
 Third lower molar with all triangles closed. *Neofiber*
 Third lower molar without closed triangles.
 Skull flat; andital bullae small. *Hyperacrius*
 Skull high; andital bullae large. *Alticola*
 Posterior border of palate continuous between maxillaries.
 Posterior border of palate straight. *Eothenomys*
 Posterior border of palate with median projection. *Antelomys*

6. KEY TO THE SUBGENERA OF MICROTUS.¹

[Based primarily on the teeth.]

- (m 1 with 6 or 7 closed triangles.)
 (Plantar tubercles 5.)
 (Small; not aquatic; fur short. *Chilotus*)
 (Large; aquatic; fur long. *Arvicola*)
 (Plantar tubercles 6. *Microtus*)
 m 1 with 5 closed triangles.
 m 3 with 3 closed triangles.
 m 3 with triangles always closed. *Neofiber*
 m 3 with triangles normally open.
 Plantar tubercles 6.
 Fur not specially modified, claws moderate.
 Posterior loop of m 3 short or strongly curved; palate normal. *Microtus*
 (Posterior loop of m 3 long and straight; palate abnormal.)
 (Skull broad and flat; plantar tubercles 5. *Hyperacrius*)
 (Skull not broad and flat; plantar tubercles 6. *Alticola*)
 (Fur very long and soft, aspect lemming-like, claws very long. *Phaiomys*)
 (Plantar tubercles 5.)
 (Small; not aquatic; fur short. *Chilotus*)
 (Large; aquatic; fur long. *Arvicola*)

¹ Characters in heavy-faced type are those of specimens with normal enamel pattern; characters in italics (inserted in parentheses) are those of specimens with abnormal enamel pattern.

m 3 with 2 closed triangles.Triangles in m 3 alternate and closed.

Aquatic; soles naked; tail long Neofiber

Not aquatic; soles hairy; tail short Lagurus

Triangles in m 3 normally opposite and open.

Claws small, those on hind feet always longest.

Mammæ 8; foot pads 5.

S small; not aquatic; fur short Chilotus

(Large; aquatic; fur long Arvicola)

(Mammæ 4; foot pads 5; skull high Pedomys)

(Claws large, those on front feet often longest.)

(Fur short and dense Pitomys)

(Fur long and soft Phaiomys)

m 1 with 4 closed triangles.m 3 with posterior loop elongated in axis of jaw.

Skull broad and flat; plantar tubercles 5 Hyperacrius

Skull not broad and flat; plantar tubercles 6 Alticola

(m 3 with posterior loop rounded or crescentic.)(m 3 with 3 closed triangles Microtus)(m 3 with 2 closed triangles Arvicola)m 1 with 3 closed triangles.(m 3 with 3 closed triangles.)

(Plantar tubercles 6.)

(Posterior loop of m 3 short or strongly curved; palate normal ... Microtus)(Posterior loop of m 3 long and straight; palate abnormal Alticola)

(Plantar tubercles 5.)

(Mammæ 8; palate normal Arvicola)

(Mammæ 4; palate abnormal Hyperacrius)

m 3 with 2 closed triangles.

Sole almost naked Arvicola

Sole hairy.

(Palate abnormal Hyperacrius)

Palate normal.

Claws long, all about equal in length Phaiomys

Claws short, those on front feet shortest Pedomys

(m 3 with 1 closed triangle Hyperacrius)m 1 with 0 closed triangles.m 2 and m 3 of approximately the same form Eothomysm 2 and m 3 very different in form Antelomys

7. KEY TO THE SUBGENERA OF MICROTUS.

[Based primarily on mammæ and foot pads.]

Mammæ 10 Phaiomys

Mammæ 8.

Plantar tubercles 6.

Palate normal Microtus

Palate abnormal Alticola

Plantar tubercles 5.

Conspicuous musk glands on sides Arvicola

No musk glands on sides.

Color dark brown Chilotus

Color light grayish or yellowish Lagurus

Mammæ 4.

Size very large.....	<i>Neofiber</i>
Size medium or small.....	
Plantar tubercles 6.....	<i>Antelionomys</i>
Plantar tubercles 5.....	
Skull not flattened.....	<i>Pedomys</i>
Skull flattened.....	
Palate normal.....	<i>Pitymys</i>
Palate abnormal.....	<i>Hyperacrius</i>

8. SUBGENERA OF *MICROTUS* GROUPED BY ESSENTIAL CHARACTERS.

Palate normal.—*Microtus*, *Pedomys*, *Pitymys*, *Chilotus*, *Phaiomys*, *Arvicola*, *Lagurus*.

Palate abnormal.—*Neofiber*, *Alticola*, *Hyperacrius*, *Eothenomys*, *Antelionomys*.

Third lower molar always with closed triangles.—*Neofiber*, *Lagurus*.

Third lower molar normally without closed triangles.—*Microtus*, *Pedomys*, *Pitymys*, *Chilotus*, *Phaiomys*, *Arvicola*, *Eothenomys*, *Antelionomys*, *Alticola*, *Hyperacrius*.

First lower molar normally with 5 closed triangles and 9 salient angles.—*Microtus*, *Chilotus*, *Neofiber*, *Lagurus*.

First lower molar normally with 3 or 4 closed triangles and 9 salient angles.—*Pedomys*, *Pitymys*, *Phaiomys*, *Alticola*, *Hyperacrius*.

First lower molar normally with 3 closed triangles and 7 salient angles.—*Arvicola*.

First lower molar without closed triangles.—*Antelionomys*, *Eothenomys*.

Third upper molar normally with 3 closed triangles and 7 to 8 salient angles.—*Microtus*.

Third upper molar normally with 2 closed triangles and 6 salient angles.—*Neofiber*, *Arvicola*, *Pitymys*, *Pedomys*, *Phaiomys*, *Chilotus*.

Third upper molar without closed triangles.—*Antelionomys*, *Eothenomys*.

Mammæ 10.—*Phaiomys*.

Mammæ 8.—*Arvicola*, *Microtus*, *Alticola*, *Chilotus*, *Lagurus*.

Mammæ 4.—*Neofiber*, *Pitymys*, *Pedomys*, *Antelionomys*, *Hyperacrius*.

Plantar tubercles 6.—*Microtus*, *Phaiomys*, *Antelionomys*, *Alticola*.

Plantar tubercles 5.—*Neofiber*, *Arvicola*, *Pitymys*, *Pedomys*, *Chilotus*, *Lagurus*, *Hyperacrius*.

DESCRIPTIONS OF LIVING GENERA AND SUBGENERA.

Genus *SYNAPTOMYS* Baird.

Synaptomys Baird, Mamm. N. Am., p. 558, 1857. Type *Synaptomys cooperi* Baird.

Geographic distribution of type species.—Boreal, Transition, and northern edge of Upper Austral Zone in eastern North America from the Atlantic coast to Minnesota.

Geographic distribution of genus.—North America from northern edge of Lower Austral Zone northward.

Essential characters:

Upper incisors with distinct longitudinal grooves.

Lower incisors with roots on inner (lingual) side of molars.

Molars rootless.

Enamel pattern characterized by great depth of reentrant angles on outer side of maxillary teeth and on inner side of mandibular teeth.

m 1 with three closed triangles and two transverse loops, or with four transverse loops and no closed triangles.

m 3 with four transverse loops and no closed triangles.

Feet not specially modified.

Soles and palms with well-developed tubercles.

Thumb with large flattened ligulate nail.

Tail very slightly longer than hind foot, terete.

External ear well developed.

Skull.—The skull of *Synaptomys* (fig. 9 and Pl. I, figs. 12, 13) is moderately broad, flat, and massive, much less so than in the other *Lemmi*. Rostrum short (nasal bones about one-fourth occipito-nasal length) and strongly deflexed; zygomatic arches not broadly flaring as in *Lemmus* and *Dicrostonyx*,¹ though more so than in the voles; middle portion of zygoma very slightly expanded, the outer surface nearly vertical; brain case not greatly broadened or flattened, and seldom if ever conspicuously ridged or furrowed; interparietal with rounded corners, the antero-posterior diameter more than half the transverse diameter; pterygoids short; interpterygoid fossa about one-sixth basilar length of skull; posterior border of bony palate ending nearly as in typical *Microtus*. (See p. 26, Pl. II, fig. 5, and fig. 7, p. 27.) Front edge of squamosal forming a narrow, shelf-like postorbital process.

Teeth.—Anterior faces of upper incisors with distinct longitudinal grooves. Lower incisor terminating posteriorly a little in front of the hinder edge of the back molar. Throughout its length each mandibular incisor lies wholly on the inner (lingual) side of the molar series. (Pl. III, fig. 1.)

The molars are all rootless. The upper molar series is about one-third the basilar length of skull, the lower series slightly less. The enamel pattern (figs. 8 and 10) is characterized by the great depth of the outer reentrant angles in the maxillary teeth and of the inner reentrant angles in the mandibular teeth. Of the maxillary teeth m 1 and m 2 show no important peculiarities of form except that the outer reentrant angles cut across to the enamel of the extreme inner side, a feature shared by *Lemmus* alone. The posterior upper molar, however, like that of *Lemmus*, differs widely from the corresponding tooth in all other *Microtinae*. It is formed of four transverse loops. The first and second of these loops are isolated by two deep reentrant angles on the outer side of the tooth, while the third is formed by an equally deep depression on the inner side. The reentrant angles and closed triangles on the inner side of the mandibular molars are greatly developed at the expense of those on the outer side. In the subgenus *Mictomys* the latter wholly disappear except in the last tooth. This has a reentrant angle near the middle, but no closed triangle.

External form.—In general appearance *Synaptomys* resembles the *Microti* much more closely than it does the *Lemmi*, a fact which has given rise to the rather inappropriate names 'lemming-vole' and 'false lemming.' The species of *Synaptomys* are thick-set microtines with large heads, ears that just appear above the moderately long fur, short tails, and small feet. In color they are all dull brownish, darker on the back, paler on the belly. The palms and soles are tuberculate, as in the voles.

General remarks.—*Synaptomys* differs from all the other genera of

¹The ratio of zygomatic breadth to basilar length is approximately 70 in *Synaptomys*, 75 in *Lemmus* and *Dicrostonyx*, and 65 in *Microtus*.

Microtina in its grooved incisors. From the other lemmings it may be known by its unmodified external form, and from the voles by the characters of its molars.

Subgenus *SYNAPTOMYS* Baird.

Synaptomys Baird, Mamm. N. Am., p. 558, 1857. Type *Synaptomys cooperi* Baird.

Geographic distribution of type species.—Boreal, Transition, and northernmost edge of Austral zone in eastern United States and adjoining British Provinces; west to Minnesota, south to Iowa, Indiana, Ohio, and Maryland.

Geographic distribution of subgenus.—Boreal zone to northern edge of Lower Austral zone in eastern Canada and eastern United States; west to Minnesota, south to Kansas and Virginia.

Essential characters:

Rostrum very heavy.

Palate nearly as in true *Microtus*.

Mandibular molars with closed triangles on outer side

Mammæ 6.

Skull.—The skull of true *Synaptomys* (fig. 9 and Pl. I, fig. 13) differs from that of *Micromys* in the remarkably heavy rostrum and in certain slight details in the form of the bony palate. The latter is almost exactly as in typical *Microtus*, the slight peculiarities in form being well within the limits of variation in the latter.

Teeth.—The incisors in true *Synaptomys* are, like the rostrum, excessively strongly built. The grooves are usually sharply defined and placed near the outer edges of the teeth.

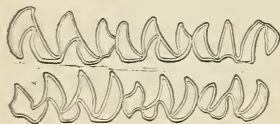


FIG. 8.—Enamel pattern of molar teeth of *Synaptomys cooperi*. (x 5.)

The maxillary teeth differ in no way from those of the species of *Micromys*. In the molars of the lower jaw, however, the outer edge of each tooth is cut by a deep reentrant angle which isolates a large outer triangle (fig. 8).

Mammæ.—The number of mammæ in *Synaptomys* has been variously recorded as four and six. Dr. Coues, in his monograph of the American *Microtina*, states that he finds six, four pectoral and two inguinal, in a female from Brookville, Ind.¹ Quick and Butler,² however, noted only four, two pectoral and two inguinal, in specimens from the same locality. Mr. Vernon Bailey records six mammæ in a female collected for the United States Department of Agriculture at Ann Arbor, Mich., and I find the same number in an alcoholic specimen taken at Rogersville, Tenn. It is probable that six is the normal number, and that Quick and Butler overlooked the posterior pair on the breast, as these are smaller than the others, at least in the alcoholic specimen from Tennessee.

¹ Monogr. N. Am. Rodentia, p. 236.

² American Naturalist, XIX, p. 114.

General remarks.—The characters distinguishing the subgenera *Synaptomys* and *Mictomys* are discussed under the latter.

Three species of true *Synaptomys* are now known: *S. cooperi* Baird, *S. fatuus* Bangs, and *S. helaletes* Merriam.¹

Subgenus MICTOMYS True.

1894. *Mictomys* True, Proc. U. S. Nat. Mus., XVII, No. 999, p. 242. Advance sheet, April 26, 1894 (full genus). Type *Mictomys innuitus* True.

1896. *Mictomys* Merriam, Proc. Biol. Soc. Washington, X, p. 57, March 19, 1896 (subgenus).

Geographic distribution of type species.—*Synaptomys innuitus* is known from the type locality only, Fort Chimo, Ungava, Labrador.

Geographic distribution of subgenus.—Hudsonian zone from Labrador to Alaska, south to northern California.

Essential characters:

Rostrum slender.

Palate not as in true *Microtus*.

Mandibular molars without closed triangles on outer side.

Mammæ 8.

Skull.—The skull of *Mictomys* is in general much like that of *Synaptomys* proper, but the whole rostral part (including incisors) is disproportionally slender and weak (fig. 9, and Pl. I, fig. 12). The bony palate is formed on the same plan as that of true *Synaptomys* or of *Microtus* proper, but differs from both of these in the prolongation of the median ridge as a spine projecting into the interpterygoid fossa.

The pterygoids are usually longer and more slender than in *Synaptomys*, and the hamular processes less strongly bent outward.

Teeth.—The incisors in *Mictomys* are much smaller in proportion to the size of the skull than in the subgenus *Synaptomys*. The grooves in the upper incisors are usually nearer the middle of the tooth, and less well defined than in true *Synaptomys*.

The maxillary teeth (fig. 10) are exactly as in the subgenus *Synaptomys*. The lower molars, however, differ from those of true *Synaptomys* in the absence of reentrant angles on the outer borders of all but the hindmost. Even in this the reentrant angle is never deep enough to isolate an outer triangle.

Mammæ.—In the type of *Synaptomys innuitus* there are eight mammæ, two more than have been recorded in *Synaptomys* proper. Whether

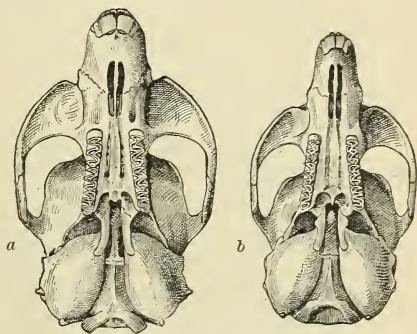


FIG. 9.—a. *Synaptomys helaletes*; b. *Synaptomys wrangeli*.

¹ See Merriam, Proc. Biol. Soc. Washington, X, p. 57, 1896.

this difference is constant or otherwise, it is, however, impossible to say.

General remarks.—*Mictomys* was first described as a full genus, but the characters on which it rests are of no more than subgeneric importance. The group is distinguished from true *Synaptomys* by the slender rostrum and incisors, slightly different form of bony palate, crenulate outer border of lower molars, and probably by the number of mammae also.

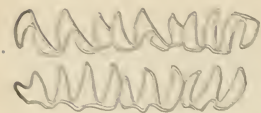


FIG. 10.—Enamel pattern of molar teeth. *Synaptomys inuitus*. (x 5.)

Four species of *Mictomys* have thus far been described, *Synaptomys inuitus* (True), *S. wrangeli* Merriam, *S. dalli* Merriam, and *S. truei* Merriam.¹

Genus LEMMUS Link.

1795. *Lemmus* Link, Zool. Beyträge, I, Pt. II, p. 75, 1795. Type by elimination *Mus lemmus* Linn.

1811. *Myodes* Pallas, Zoogr. Rosso-Asiat., I, p. 172, 1811 (part).

1877. *Myodes* Coles, Monogr. N. Am. Rodentia, p. 237, 1877, and most subsequent authors.

Geographic distribution of type species.—Arctic region in Asia and eastern Europe.

Geographic distribution of genus.—Arctic region in both hemispheres.

Essential characters:

- Upper incisors without grooves.
- Lower incisors with roots on inner (lingual) side of molars.
- Molars rootless.
- Enamel pattern as in *Synaptomys*.
- Feet highly modified.
- Palms and soles without well-developed tubercles.
- Thumb with large flattened 'strap-shaped' nail.
- Tail shorter than hind foot, terete.
- External ear small but well developed.

Skull.—The skull of *Lemmus* (Pl. I, fig. 6) is perhaps the most highly modified in the family *Microtinae*. The rostrum, like that of *Synaptomys*, is short in proportion to the length of the skull (nasal bones contained about three and one-half times in occipito-nasal length), the dorsal profile bent abruptly downward. Zygomatic arches very abruptly and broadly flaring, each expanded near the middle into a wide, strongly oblique plate.² Brain case broad, flat, and subquadrate in outline, but dwarfed in appearance by contrast with the large zygomata. Pterygoids short (about as in *Synaptomys*). Bony palate terminating essentially as in *Synaptomys*, but lateral pits very deep and anterior

¹ See Merriam, Proc. Biol. Soc. Washington, X, p. 61, 1896.

² These plates may be nearly 5 mm. across in the widest part.

edge of interpterygoid fossa carried forward over (dorsad to) overhanging edge of palate (Pl. II, fig. 14). The anterior edge of the squamosal forms a narrow but distinct shelf-like postorbital process, much as in *Synaptomys*, but more strongly developed.

Teeth.—The dentition of *Lemmus* is essentially the same as that of *Synaptomys*. The upper incisors are, however, much more slender in proportion to the size of the skull, and are without the peculiar grooves always present in *Synaptomys*. In the pattern of enamel folding, the only difference between the two genera is that the third transverse loop in the hindermost maxillary tooth is isolated by a single reentrant angle in *Synaptomys*, and by the contact of two reentrant angles in *Lemmus* (fig. 11).

External form.—In external form the species of *Lemmus* differ very widely from all other microtines except *Dicrostonyx*. The head is disproportionately large for the short thick body,¹ while the tail is reduced to a mere rudiment only about two-thirds as long as the hind foot. The feet are highly modified to fit the animals to their fossorial habits. While the hind feet are unusually large and strong, the front feet are even more specialized. The thumb is provided with a large ligulate nail and the fingers are armed with long, sharp claws (fig. 12). The claws are, however, simple in form and are not subject to the periodic changes that occur in those of *Dicrostonyx*.

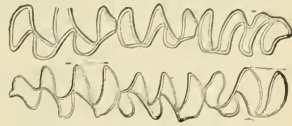


FIG. 11.—Enamel pattern of molar teeth, *Lemmus lemmus*. (x 5.)



FIG. 12.—Left front foot, *Lemmus lemmus* (hair removed).

In the alcoholic specimens that I have examined the palms show no trace of tubercles, but the soles bear indications of several very small and exceedingly rudimentary pads close to the base of the toes. The fur is remarkably long and dense, the palms and soles densely furred, and the tail provided with a pencil of stiff bristle-like hairs longer than the tail vertebrae.

General remarks.—The species of *Lemmus* are true lemmings with highly modified skull and external form. With these characters they combine the dentition of *Synaptomys* without, however, the peculiar incisors of the latter. *Lemmus* differs from *Synaptomys* in its highly modified skull and external form as well as in the dental character just mentioned. From *Dicrostonyx* it is distinguished by cranial and dental characters and by the well-developed external ears (fig. 15), as well as by the simple claws and large thumb nail.

The species of *Lemmus* at present recognized are *L. lemmus* (Linnaeus), *L. obensis* (Brants), *L. schisticolor* (Lilljeborg), and *L. nigripes* (True).

¹ This peculiarity is carried even further in *Lemmus* than in *Synaptomys*.

Genus DICROSTONYX Gloger.

1830. *Cuniculus* Wagler, Nat. Syst. d. Amphibien. p. 31, 1830 (part).
 1877. *Cuniculus* Cones, Monogr. N. Am. Rodentia, p. 243, 1877.
 1841. *Dicrostonyx* Gloger, Gemeinn. Hand- u. Hilfsbuch d. Naturgesch., pp. XXXI, 97,
 1841. Type, an American species, probably *Mus hudsonius* Pall.
 1854. "*Myolemmus* Pomel, Ann. Sci. Soc. Auvergne, 1854" (fide Trouessart).
 1855. *Misothermus* Hensel, Zeitschr. der Deutsch. geolog. Gesellsch., VII, p. 492, 1855.
 Type *Myodes torquatus* Pall.
 1881. *Borioikon* Polyakoff, Mém. Acad. Imp. Sci. St. Petersburg, XXXIX, suppl. p. 34,
 1881. Type *Myodes torquatus* Pall.

Geographic distribution of type species.—Arctic America.

Geographic distribution of genus.—Arctic region in both hemispheres.

Essential characters:

Upper incisors without grooves.

Lower incisors with roots on inner (lingual) side of molars.

Molars rootless.

Enamel pattern characterized by approximate equality of reentrant angles.

m 1 with 7 closed triangles and 2 transverse loops.

m 3 with 3 or 4 closed triangles and 2 transverse loops.

Feet highly modified.

Palms smooth; soles with rudimentary tubercles.

Thumb with a rudimentary nail.

Tail shorter than hind foot, terete.

External ear rudimentary.

Skull.—The skull of *Dicrostonyx* (Pl. I, fig. 14) in a general way resembles that of *Lemmus*, but is smaller and more lightly built. The zygomata are less broadly flaring and the expansion near the middle is comparatively slight. The outer face of the expanded portion, as in *Lemmus*, is strongly oblique. The rostrum is also lighter and more slender. While the pterygoids are proportionally longer than in *Lemmus*, the posterior edge of the bony palate is formed exactly as in the latter (Pl. II, figs. 12 and 14). The anterior edge of the squamosal

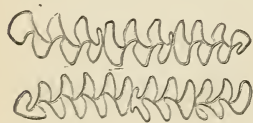


FIG. 13.—Enamel pattern of molar teeth, *Dicrostonyx* from Ungava, Labrador. (x 5.)

gives off a conspicuous peg-shaped postorbital process very different from the postorbital process in *Lemmus* or any of the other *Microtine*. These pegs are especially conspicuous when the skull is viewed from the ventral aspect.

Teeth.—Incisors essentially as in *Lemmus*. Molars rootless. Pattern of enamel folding (fig. 13) very different from that of either of the other genera of *Lemmi* and in some respects resembling that of the *Microti*. The reentrant angles on the opposite sides of the teeth are approximately equal in depth, thus producing closed triangles of nearly the same size on the two sides. The first lower molar contains seven closed triangles in addition to a transverse loop at each end. The second lower molar contains a posterior loop followed by four alternating closed triangles and an anterior transverse loop, which is much flattened

and so small that the tips of the salient angles do not reach to the level of the tips of the other salient angles of the tooth. Occasionally the anterior outer triangle opens into the transverse loop. The posterior lower molar has a posterior transverse loop followed by three large closed or nearly closed triangles (two on the inner side), and a fourth smaller triangle on the outer side.¹ The maxillary teeth have each a large anterior loop. This is followed in the first by five alternating closed triangles and a small postero-external loop, in the second by four closed triangles and a small postero-external loop, and in the third by four closed triangles and a small rounded terminal loop.

External form.—In external form the species of *Dicrostonyx* are even more specialized than the members of the genus *Lemmus*. As in the latter, the head is very large, the tail is reduced to a stub, shorter than the hind foot, and the feet are highly modified for digging.

The external ears are, however, mere naked folds of integument lying just behind the meatus (fig. 14 *a*). The fur is long and dense, much as in *Lemmus*. The palms and soles are densely furred, and the tail is provided with a stiff pencil of bristle-like hairs, longer than the tail vertebræ. The hind feet are very broad, the breadth at base of toes being about one-half length of foot.² On the hind foot there are several minute, faintly developed tubercles near the base of the toes. The palms are,

however, perfectly smooth. The claws on the hind feet are large and well formed, though in no way different from those of *Lemmus*. Those on the front feet are very highly modified, and present seasonal changes in size and form unknown elsewhere among the *Microtina*. The thumb (fig. 15) is greatly reduced in size. The thumb nail is so small as readily to escape notice, but the ball of the thumb projects as a distinct tubercle, the surface of which

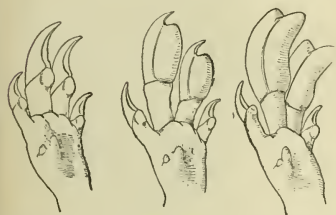


FIG. 15.—Left front foot of three specimens of *Dicrostonyx* from Alaska, showing successive stages in the development of the claws (hair removed).

is covered with a thick layer of corneous tissue. The claws on the second and fifth fingers are large, though not peculiar in form. The two middle claws, on the contrary, while in summer not different from those of *Lemmus*, are in winter very greatly enlarged (fig. 15), and

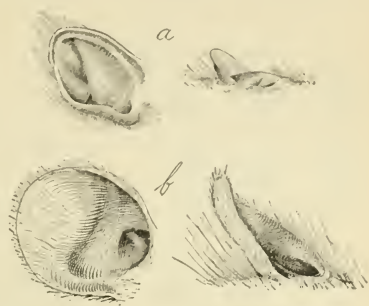


FIG. 14.—Ear, (*a*) *Dicrostonyx*, (*b*) *Lemmus* (double natural size).

¹ In *Dicrostonyx torquatus* there is a minute supplemental anterior internal loop which is absent in the species that occurs in Labrador.

² In *Lemmus* this breadth is only about one-third length of foot.

wholly unlike those of any other microtine. Dr. Cones's description of the claws of *Dicrostonyx* is so interesting that it may be quoted almost entire. He says (Monogr. N. Am. Rodentia, pp. 248, 249):

The two middle fore claws attain their maximum of development in winter. In spring and early summer these claws do not appear very different from those of *Myodes* [= *Lemmus*], though averaging larger, more bulbous at base underneath, with the terminal portion slenderer, straighter, and sharper. This bulbous portion underneath grows out simultaneously with increase in length and amount of curvature of the main portion of the claw, until it equals or even exceeds the length of the latter, and is quite as stout, or even stouter, being somewhat broad and pad-like. At this period it runs the whole length of the claw, from which it is separated by a groove along the sides, and by a notch at the end, both of varying depth. The claw then looks nearly like two claws, one underneath the other. The pad would then seem to gradually sever its connection with the main claw by progressive increase in depth of the constriction marked by the lateral groove and terminal notch, as well as by loosening from the base, when it appears like an excrescence; it is finally lost. Thus the process appears to be a periodical one, like the shedding of the horns of ruminants, and not continually progressive with age; and would seem to be connected with the particularly fossorial habits of the quasi-hibernating animal that digs galleries under ground in which to reside during the cold season, as compared with its freer and more active mode of life in summer. At the period of the maximum development of the claws these equal or surpass half an inch in length. * * *

General remarks.—*Dicrostonyx* is so readily distinguished by its peculiar dentition, highly modified feet, and rudimentary external ears, that it requires no detailed comparison with any other genus.

While *Dicrostonyx torquatus* (Pallas) is the only species now recognized, there are doubtless several others.

Genus PHENACOMYS Merriam.

1889. *Phenacomys* Merriam, North American Fauna No. 2, p. 28, October 30, 1889.

Geographic distribution of type species.—*Phenacomys intermedius* is known only from the type locality, Kamloops, British Columbia.

Geographic distribution of genus.—Boreal North America; also recorded from the bone breccia of Beremend, southern Hungary, and the Forest Beds of Norfolk and Suffolk, England (Nehring, Naturwissenschaftliche Wochenschrift, Nr. 28, p. 346, July 15, 1894).¹

Essential characters:

Upper incisors without grooves.

Lower incisors with roots on outer side of molars.

Molars rooted.

Enamel pattern characterized by approximate equality of reentrant angles in maxillary teeth and great depth of reentrant angles on inner side of mandibular teeth.

m 1 with five closed triangles.

m 3 with two or three closed triangles.

¹ I have not seen the original description of the remains from Beremend (described by Nehring in Naturwissenschaftliche Wochenschrift, 1883). The teeth from the Forest Beds represent an animal which is certainly not *Phenacomys*. (See note on *Arvicola intermedius* Newton on page 75.)

Bony palate not terminating in a thin-edged shelf continuous between alveoli of posterior incisors.

Feet not specially modified.

Thumb with a small pointed nail.

Tail longer than hind foot, terete.

Fur not specially modified.

Skull.—The skull of *Phenacomys* (Pl. I, fig. 5) differs very slightly in general form from that of typical *Microtus*. The brain case is, however, flatter and more quadrate (but no more so than in the subgenera *Lagurus* and *Pitymys*), and the zygomata bend down somewhat more abruptly in front. The expansion of the zygoma at the region of contact between the malar and the zygomatic process of the maxillary is rather more abrupt than is usual in *Microtus*, but the difference is very trifling. The post-orbital processes of the squamosals are slightly more prominent and angular than in *Microtus arvalis* or *M. pennsylvanicus*, but scarcely more developed than in *M. agrestis*, and considerably less so than in *M. allenii*. The audital bullae are proportionally about the same size as or slightly smaller than in *Microtus arvalis*. They are more globular and less 'subfusiform' than in the typical species of true *Microtus*, but closely resemble those of *M. agrestis*. The palate (Pl. II, fig. 1) is formed essentially as in the members of the subgenus *Lagurus* (Pl. II, figs. 3 and 4).

Teeth.—The teeth of *Phenacomys* differ in many ways from those of the other voles. In young individuals the molars (fig. 16) are rootless, but by the time the animals are full grown each molar has developed two distinct roots, which, however, remain open until an advanced age, though not so long as in the genus *Erotomys*. The pattern of enamel folding (fig. 17) is essentially the same as that of the voles of the subgenera *Pedomys* and *Phaiomys*. (See pp. 56 and 57.) The differences are to be found in the lower molars where the reentrant angles on the inner side are proportionally deeper and those on the outer side proportionally shallower than in *Pedomys*. There is a corresponding difference in the size of the closed triangles on the opposite sides of the teeth. The anterior outer loop in the second lower molar is especially reduced.

FIG. 17.—Enamel pattern of molar teeth, *Phenacomys oclatus*. (x 5.)

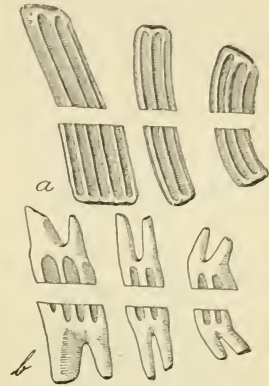


FIG. 16.—Side view of molars, *Phenacomys*. (a) young, (b) adult. (x 3.)

In *Phenacomys* the root of the lower incisor runs back between the roots of the second and third molars, and terminates on the outer side of the tooth row in the ascending ramus of the jaw, at about the level of the middle of the posterior molar, and distinctly below the dental foramen. (Pl. III, fig. 2.) While exactly this condition is not found elsewhere except in *Erotomys*, it is somewhat closely approached in *Fiber*.

External form.—In external form the species of *Phenacomys* show no peculiarities to distinguish them from the other voles. The body, tail, feet, ears, and eyes are usually proportioned about as in *Microtus arralis* or *M. austerus*. In *P. longicauda*, however, the tail is proportionally longer than in any of the other known species.

General remarks.—*Phenacomys* is readily distinguished from *Microtus* by the rooted molars. From *Erotomys*, *Phenacomys* is separated by certain characters in the form of the skull, and more especially of the bony palate, as well as by peculiarities in the teeth. The differences between the three genera may be compared in detail as follows:

<i>Microtus.</i>	<i>Erotomys.</i>	<i>Phenacomys.</i>
Root of lower incisor above dental foramen.	Root of lower incisor below dental foramen.	Root of lower incisor below dental foramen.
Molars rootless throughout life..	Molars rooted in the adult, the roots closed in extreme old age.	Molars rooted in the adult, the roots closed in extreme old age.
Molars large and strong, the salient angles sharp.	Molars small and weak, the salient angle rounded.	Molars large and strong, the salient angles sharp.
Reentrant angles on outer and inner sides of lower molars approximately equal in depth.	Reentrant angles on outer and inner sides of lower molars approximately equal in depth.	Reentrant angles on inner side of lower molars very much deeper than those on outer side.
Skull strong and angular.....	Skull weak and rounded.....	Skull strong and angular.
Posterior border of bony palate extremely variable.	Posterior border of bony palate a thin-edged shelf continuous between alveoli of posterior molars.	Posterior border of palate never a thin-edged shelf.
Middle portion of zygoma distinctly expanded.	Middle portion of zygoma scarcely expanded.	Middle portion of zygoma distinctly expanded.

Since the discovery of the genus *Phenacomys* the following species have been described: *P. intermedius* Merriam, *P. celatus* Merriam, *P. ungava* Merriam, *P. latimanus* Merriam, *P. orophilus* Merriam, *P. longicauda* True, *P. truei* Allen, and *P. oramontis* Rhoads. The status of these forms is wholly a matter of conjecture.

Genus EVOTOMYS Coues.

1839. *Myodes* DeSélys Longchamps, Études de Micromammalogie, p. 87, 1839 (section).

1883. *Myodes* Lataste, Le Naturaliste, Tome II, p. 349, 1883 (subgenus).

1840. *Hypudæus* Keyserling and Blasius, Die Wirbelthiere. Europas, p. 34, 1840 (subgenus). Type *Mus glareolus* Schreber. (Not *Hypudæus* Illiger, 1811.)

1857. *Hypudæus* Baird, Mamm. N. Am., p. 513, 1857 (subgenus).

1874. *Erotomys* Coues, Proc. Acad. Nat. Sci. Phila., p. 186, 1874 (genus). Type *Mus rutilus* Pall

Geographic distribution of type species.—Arctic region in Europe and Asia, possibly in America also.

Geographic distribution of genus.—Boreal North America, Asia, and Europe.

Essential characters:

- Upper incisors without grooves.
- Lower incisors with roots on outer side of molars.
- Molars rooted.
- Enamel pattern characterized by approximate equality of reentrant angles.
- m 1 with five closed or nearly closed triangles.
- m 3 with three closed triangles.
- Feet not specially modified.
- Thumb with a small, pointed claw.
- Pin not specially modified.
- Tail longer than hind foot, terete.

Skull.—The skull of *Evotomys* (Pl. I, fig. 4), as compared with that of the other voles, is characterized by a general weakness and lack of angularity. All the outlines are full and rounded, and the ridges and furrows are slightly developed, even in extreme old age. The interorbital region is broader and the audital bullae are larger and more inflated than usual in *Microtus* and *Phenacomys*. On the other hand, the zygomata are very slender and scarcely widened in the region of contact between the jugal and the zygomatic process of the maxillary. The mandible also is slender and weak. The bony palate terminates in a thin-edged shelf, continuous between the alveoli of the posterior incisors (fig. 7 and Pl. II, fig. 10). The structure is very different from that found in *Phenacomys* and in typical *Microtus*.¹

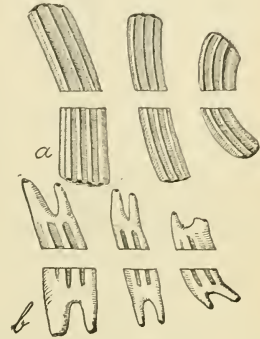


FIG. 18.—Side view of molars, *Evotomys*. (a) young, (b) adult. (x 3.)

Teeth.—The incisors are exactly as in *Phenacomys*. The lower incisor runs back along the lingual side of the first and second molars, but crosses the line of the molar tooth row between the second and third molars, terminating in the ascending ramus of the mandible at about the level of the middle of the posterior molar and distinctly below the dental foramen. The molars are rootless in the young (fig. 18), but in the adult each is provided with two distinct roots which eventually become fully closed.² In one very old individual the crowns of the lower molars are completely worn away, so that each root, with the exception of the anterior root of m 3 (which has been shed) stands alone like a simple, round-topped tooth (Pl. III, fig. 4). The molars are all very narrow and weak, in this character strongly contrasted with the strong, broad teeth of *Microtus* and *Phenacomys*.

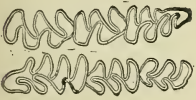


FIG. 19.—Enamel pattern of molar teeth, *Evotomys gapperi*. (x 5.)

¹ For detailed comparison of the palates of *Evotomys* and *Microtus* see pages 26–28.

² In the original description of the genus *Phenacomys* (North Am. Fauna No. 2, p. 30) it is stated that “*Phenacomys* has genuine rooted molars, not half-rooted molars like those of *Evotomys*, which grow from persistent pulps.” *Evotomys*, however, has as perfectly rooted molars as *Phenacomys*, though the roots do not close so early in life.

In the number and arrangement of triangles the enamel pattern (fig. 19) is the same as that of the tetramerodont species of *Microtus* (see p. 65). The salient angles are, however, for the most part rounded, and so placed that the triangles are seldom fully closed.

External form.—In external form *Erotomys* does not differ essentially from *Microtus*, although the ears are usually larger. The red or rufous color of most of the species gives them a very different appearance from the other voles.

General remarks.—The characters which separate *Erotomys* from *Microtus* and *Phenacomys* have been presented in such detail under the latter that it is unnecessary to consider them further. The peculiar bony palate of *Erotomys* has been considered one of the best generic characters. Since the discovery that it is perfectly reproduced in two subgenera of *Microtus* (*Antelomys* and *Eothenomys*) it loses much of its importance.

The genus *Erotomys* is represented in Europe, Asia, and North America by numerous species and subspecies whose interrelationships are at present little understood. Among the American species may be mentioned *E. gapperi* (Vigors), *E. fuscodorsalis* Allen, *E. galei* Merriam, *E. idahoensis* Merriam, *E. californicus* Merriam, and *E. occidentalis* Merriam; among those found in the Old World are *E. rutilus* (Pallas), *E. glareolus* (Schreber), and *E. rufocanus* (Sundevall).

Genus MICROTUS Schrank.

1798. *Microtus* Schrank, Fauna Boica, I, 1ste Abth., p. 72, 1798. Type by elimination *Microtus terrestris* Schrank = *Mus arvalis* Pall.

1883. *Microtus* Lataste, Le Naturaliste, Tome II, p. 348, 1883.

1801. *Arvicola* Lacépède, Mém. de l'Institut, III, p. 489, 1801. Type '*Arvicola amphibius*' = *Mus terrestris* Linn.

Geographic distribution of type species.—Central Europe and parts of Asia.

Geographic distribution of genus.—In both hemispheres the genus *Microtus* ranges from near the northern limit of mammalian life to the edge of the tropics.

Essential characters:

Upper incisors without grooves.

Lower incisors with roots on outer side of molar series.

Molars rootless.

Enamel pattern characterized by approximate equality of reentrant angles.

m 1 usually with five closed or nearly closed triangles.

m 3 with one, two, or three closed triangles.

Tail nearly always longer than hind foot, terete.

Feet, fur, eyes, and ears very variable.

Thumb never with a well-developed ligulate nail.

Skull.—The skull of *Microtus* varies greatly in shape among the different subgenera. Full descriptions will be given under each of these. Considering the genus at large it is difficult to frame any diagnosis by which the skull may be in every case distinguished from that of the other voles. Most of the characters which at various times have been

brought forward for this purpose prove to be either wholly inconstant or constant only when particular subgenera are held in view.

Teeth.—Although the skull of *Microtus* presents no tangible diagnostic characters, the teeth are readily distinguishable from those of all other members of the subfamily. The upper incisors are never grooved except in occasional abnormal specimens. The root of the lower incisor crosses the line of the molar series between the second and third molars, causing a greater displacement of the roots of the latter (Pl. III, fig. 3) than occurs in any other genus. It terminates in the ascending ramus of the mandible at a point slightly above and behind the dental foramen (Pl. III, fig. 3). The molars, even in extreme old age, are never rooted (fig. 20). This character alone distinguishes them from the molars of the other voles. The pattern of enamel folding varies considerably in the different subgenera, and forms one of the numerous characters by which the latter may be separated. Detailed descriptions of the enamel patterns are given in the accounts of the subgenera.

External form.—In external form the members of the genus *Microtus* vary excessively. Some resemble lemmings so closely that they have been associated with these by certain writers. Others are modified for an aquatic life and in consequence have more the appearance of muskrats (*Fiber*). Still others pass most of their time under ground. In these the ears, eyes, and tail are reduced, the front feet enlarged, and the fur so modified as to suggest that of the moles. The great majority of species, however, show none of these special adaptations, but resemble in a general way the members of the genera *Phenacomys* and *Erotomys*. Whatever may be the modifications in form, the tail is almost invariably longer than the hind foot and the thumb is armed with a small or rudimentary pointed nail (fig. 21).



FIG. 21.—Left front foot, *Microtus terrestris*.

General remarks.—The characters of *Microtus*, as contrasted with *Erotomys* and *Phenacomys*, have already been given (p. 42) and need not be repeated here.

Subgenus EOTHENOMYS¹ Miller.

New subgenus. Type *Arvicola melanogaster* Milne-Edwards.

Geographic distribution of type species.—Moupin, western Szechuen, and western Fokien, China. (Blanford.)

Geographic distribution of subgenus.—*Microtus melanogaster* is the only known species of *Eothenomys*, hence the geographic distribution of the subgenus is the same as that of the type species.

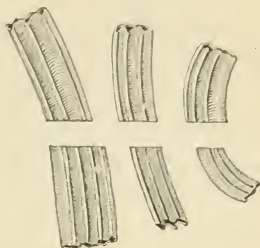


FIG. 20.—Side view of molars of adult *Microtus allenii*. (x 2.)

¹Ἠώς, the morning (eastern); ἔεν, from; μῦς, mouse.

Essential characters:

Palate abnormal.

m 3 without closed triangles.

m 1 with triangles frequently open and 8 or 9 salient angles.

m 3 with triangles usually open and 6 salient angles.

Mammæ (number not known).

Plantar tubercles, 5.

Sole hairy.

Claws on hind feet longest.

Fur apparently somewhat modified.

Skull.—In the specimens of *Eothenomys* that I have examined the skull is not in sufficiently good condition to permit of any detailed description. The peculiar structure of the bony palate taken in connection with the teeth is, however, of itself enough to characterize the group.

Bony palate.—Unfortunately in the two specimens of *Microtus melanogaster* that I have seen (82.6.16.11 and 92.10.12.5, British Museum Register) the basal part of the skull is so injured that the form of the interpterygoid fossa can not be determined.

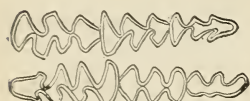


FIG. 22.—Enamel pattern of molar teeth, *Microtus (Eothenomys) melanogaster*. (x 5.)

The bony palate, however, is sufficiently preserved to show the essential details of its structure (Pl. II, fig. 11). That part of the palate which lies in the level of the roof of the mouth ends abruptly opposite the front end of the back upper molar in a straight-edged shelf which extends without notch or projection from alveolus to alveolus. Although the form is thus strikingly different from that of the typical microtine palate, the vestiges of the structure there present may still be recognized. The lateral grooves and median ridge are present, though slightly developed. The former terminate in two depressions lying just in front of the wide, flat, lateral bridges which completely obliterate the posterior ends of the grooves, and together with the terminal part of the median ridge form the edge of the palatal shelf. The palate in all its essential characters is thus exactly like that of *Erotomys*.

Enamel pattern in general.—The enamel pattern in *Eothenomys* (fig. 22) is in many ways remarkable. The triangles in all the teeth tend to remain open, the points of the salient angles are blunt and rounded as in *Erotomys*, the triangles on the outer and inner sides of the teeth are subequal in size, and the maxillary teeth are especially noticeable for their likeness to each other. The figures published by Blanford¹ fail to do justice to the teeth of this species. These are better represented in Milne-Edwards's original plate,² in which there is also a hint at the palate structure.

¹Journ. Asiatic Soc. Bengal, L, pt. II, Pl. II, fig. A.

²Recherches p. servir à l'histoire nat. d. Mammifères, Vol. I, Pl. XLVI, figs. 1c and 1d.

Front lower molar.—The first lower molar has the usual transverse posterior loop and a moderately long rounded anterior loop, with a strong salient angle at each side of the base. It has five lateral triangles, three on the inner side, two on the outer side. These may be perfectly isolated, or more often widely open. Except for the greater tendency to equality in the triangles, the teeth in the lower jaw do not differ very greatly from the mandibular teeth of true *Microtus*.

Back upper molar.—The posterior maxillary tooth most nearly resembles that of *Pedomys*. The anterior loop is followed by two lateral triangles, subequal in size and more or less completely isolated from each other and from the anterior loop. The third lateral triangle is reduced to a strongly developed salient angle on the inner side of the posterior transverse loop. A second salient angle is formed on the outer side of this loop, which thus appears as a crescent joined near the middle of its concavity to the rest of the tooth.

Other teeth.—The middle upper molar has a postero-internal loop nearly as large as the postero-external loop, the two placed opposite each other. The result is a tooth of practically the same shape as the one behind it. The anterior upper molar is likewise provided with a very large postero-internal loop opposite the loop on the outer side, normally terminating the tooth. Thus it very closely resembles the two other maxillary teeth, differing only in its one more closed triangle at the front end.

Mammae.—The number of mammae in *Eothenomys* is unknown.

Feet.—The feet are moderately hairy, in this respect not differing from true *Microtus*. Blanford states that there are five well-developed pads on the sole and a rudimentary sixth. The claws are not greatly developed on any of the feet; those on the hind feet are the longest.

Fur.—A skin in the British Museum has the fur of a peculiar, dense, mole-like quality suggestive of *Pitymys*. The specimen appears to be in worn coat, however, and this character may not be normal.

General remarks.—*Eothenomys* is such a well-marked subgenus that it is surprising to find that it has hitherto received no name. In tooth pattern it agrees in a general way with *Microtus sikkimensis*, a circumstance which induced Blanford to place it in the subgenus '*Neodon*;' but the palate structure is widely different from that of the subgenus *Microtus*, to which *M. sikkimensis* really belongs, while the similarity in the enamel pattern of the two species is very superficial.

Subgenus ANTELIOMYS¹ Miller.

New subgenus. Type *Microtus chinensis* Thomas.

Geographic distribution of type species.—*Microtus chinensis* is known from one specimen collected at Kiating-fu, west Sze-chuen, China.

¹ Ἀντιλίος, eastern; μῦς, mouse.

Geographic distribution of subgenus.—*Microtus chinensis* is the only known species of the subgenus.

Essential characters:

Palate abnormal.

m 3 without closed triangles.

m 1 with triangles mostly open, and with 9 salient angles.

m 3 with triangles mostly open, and with 9 salient angles.

Mammae, 4.

Plantar tubercles, 6. ^

Sole moderately hairy.

Claws on hind feet longest.

Fur not specially modified.

Skull.—As remarked by Mr. Thomas in the original description of *Microtus chinensis*, the skull of *Antelionomys* resembles in a general way that of *Erotomys*. Unfortunately, I am unable to add any more definite information concerning its characters.

Bony palate.—The palate of *Antelionomys* (Pl. II, fig. 8) is similar to that of *Eothenomys*, except that the median ridge is produced backward as a distinct spike lying perfectly in the plain of the roof of the mouth.

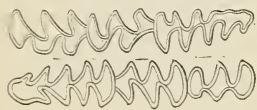


FIG. 23.—Enamel pattern of molar teeth, *Microtus (Antelionomys) chinensis*. (x 5.)

Just in front of the strongly developed lateral bridges, the posterior edges of which form the back rim of the bony palate, lie two pits, in which terminate the lateral grooves. These pits communicate freely over (dorsad to) the lateral bridges with the anterior end of the broad mesopterygoid fossa.

Enamel pattern in general.—The enamel pattern in *Antelionomys* (fig. 23) is characterized by rounded angles, imperfectly closed triangles, and great complexity in the prisms of the back upper molar.

Front lower molar.—The anterior lower molar is made up of four transverse, perfectly isolated loops. The anterior loop is much the largest and contains three salient angles (two on the inner side). Each of the succeeding loops has two salient angles. The tooth thus contains exactly the same elements as the corresponding one in *Microtus*, the difference in form being due to the fact that in *Antelionomys* the prisms are placed opposite each other instead of alternately. The prisms on the opposite sides of the tooth are nearly equal in size, thus producing the bilaterally symmetrical appearance found to a less degree developed in *Alticola* and *Eothenomys*. The figures in the original description of *Microtus chinensis*¹ give a very poor idea of the teeth.

Back upper molar.—The posterior maxillary tooth is like that of true *Microtus* except that the posterior loop is greatly lengthened and on the lingual side cut by two reentrant angles, of which the anterior is

¹ Ann. & Mag. Nat. Hist., Ser. 6, Vol. VIII, p. 118, August, 1891.

the deeper. There is a salient angle at the outer base of the posterior loop and the outer border is faintly crenulate. A tooth with nine well-developed salient angles is the result.

Other teeth.—The front maxillary teeth are exactly as in tetramerodont *Microtus*. The back molars of the lower jaw are likewise in no way peculiar. They both, however, have the prisms on the two sides opposite, thus lacking all closed triangles.

There is nothing worthy of note in the form of the incisors.

Mammæ.—In the unique type specimen of *Microtus chinensis*, which is a female, there are four teats, all inguinal.

Feet.—The sole is well haired from heel to tubercles. There are six pads on the sole, all well developed.

Fur.—The fur is not specially modified.

General remarks.—In its palate structure *Antelionomys* is related to *Eothenomys*, and more remotely to *Alticola*, together with which it bridges the gap (so far as the palate alone is concerned) between *Microtus* and *Erotomys*. These facts were in part noticed by Mr. Thomas, who says in the original account of *M. chinensis*:

In some respects it seems to be annectent between *Erotomys* and the rest of the voles, the structure of its palate and some of its dental characters [opposite prisms and rounded angles] showing striking affinities to the former, far as its rootless teeth, fewer mammae, and different external form separate it from any of the known members of that group.

The enamel pattern is, however, very different from that of *Erotomys*, while the resemblance to that of its nearest relative, *Eothenomys*, is almost equally remote.

Microtus chinensis is the only species of *Antelionomys* thus far known, unless *Microtus middendorffii* (Polyakoff)¹ from Siberia² proves to be a member of the same group. The figure of the teeth in the original description of *M. middendorffii* is suggestive of *Microtus chinensis*, though the triangles are very strongly isolated. Neither the palate structure nor the number of mammae is given by Polyakoff, so it is impossible to come to any conclusion on the subject of the animal's true status.

Subgenus LAGURUS Gloger.

1841. *Lagurus* Gloger, Gemeinn. Hand-u. Hilfsbuch d. Naturgesch., p. 97, 1841 (genus). Type, *Lagurus migratorius* Gloger = *Mus lagurus* Pallas?³
1895. *Lagurus* Merriam, Am. Naturalist, XXIX, p. 758, Aug., 1895 (subgenus).

¹ Mém. Acad. Imp. Sci., St. Pétersbourg, XXXIX suppl., p. 70, 1881.

² Polyakoff gives the following localities: Taimur, Vilui River, Ayan, and Kara River.

³ In restoring the generic name *Lagurus* (Ann. & Mag. Nat. Hist., 6th ser., XV, Feb. 1, 1895) Mr. Thomas gives the species *lagurus* as the type. It appears highly probable, however, that Gloger's *Lagurus migratorius* is the *Hypudæus migratorius* of Lichtenstein (Eversmann's Reise nach Buchara, p. 123, 1823) = *Microtus* (*Lagurus*) *luteus* (Eversmann).

1881. *Eremiomys* Polyakoff, Mém. Acad. Imp. Sci., St. Pétersbourg, XXXIX suppl., p. 34, 1881 (genus). Type *Mus lagurus* Pall.

Geographic distribution of type species.—Plateaus of western and central Asia.

Geographic distribution of subgenus.—The range of the subgenus *Lagurus* is very imperfectly known, but probably extends over a large part of the Boreal region in Asia and in western North America.

Essential characters:

Palate slightly abnormal.

m 3 normally with 2 or 3 tightly closed triangles.

m 1 normally with 5 closed triangles and 8 or 9 salient angles.

m 3 normally with 2 or 3 closed triangles and 5 or 6 salient angles.

Mammæ, 8.

Plantar tubercles, 5.

Sole very hairy.

Claws on hind feet longest.

Fur not specially modified.

Skull.—The skull of *Lagurus* (Pl. I, fig. 7¹) may be at once recognized by the form of the audital bullæ (fig. 24). These are larger than in any other subgenus of *Microtus*, and are especially remarkable on account of the way in which they project backward behind the plane of the occiput. Aside from the audital bullæ, the skull does not differ very noticeably from that of *Pitymys* or *Chilotus*. As compared with that of *Pitymys*, however, the rostrum is considerably more slender. The dorsal outline is flat, as in *Chilotus*.

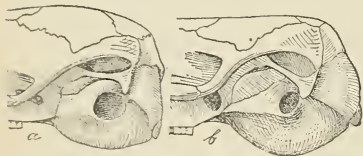


FIG. 24.—Audital bullæ, (a) *Microtus* (*Microtus*) *arvalis*; (b) *M. (Lagurus) pallidus*. (x 2.)

Bony palate.—The bony palate (Pl. II, fig. 2) is normal in structure but

there is less difference than usual between the levels of the portions lying in front of and behind the lateral bridges. A peculiar flat palate with shallow lateral pits and broad, ill-defined median sloping ridge is the result. This form of palate is much like that of *Phenacomys* (Pl. II, fig. 1).

Enamel pattern in general.—The enamel pattern of *Lagurus* (fig. 25) is characterized by the tight closure of all triangles, notably in the back lower molar, and the great width of the reentrant angles. The latter peculiarity gives the

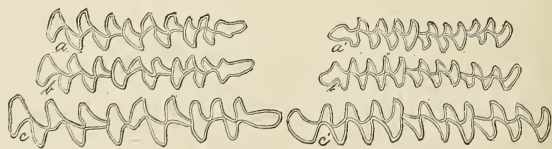


FIG. 25.—Enamel pattern of molar teeth: (a) *Microtus (Lagurus) pallidus*; (b) *M. (L.) lagurus*; (c) *M. (L.) luteus*. (x 5.)

¹See also Naturwissenschaftliche Resultate der von N. M. Przewalski unternommenen Reisen, Pl. XIII, figs. 1, 2, 3, 12, 13, and 14.

teeth a drawn-out appearance, which is highly characteristic. Wide reentrant angles occur in the teeth of the young of all *Microti*; in *Lagurus* this embryonic character is retained by the adults.

Front lower molar.—The number of loops and triangles in the first mandibular tooth is the same as in true *Microtus*. In *Microtus przewalskii* and *Microtus luteus* the anterior loop is simple and much reduced, while in *Microtus lagurus* and *M. pallidus* the loop is exactly as in *Microtus arvalis*.

Back upper molar.—The posterior maxillary tooth differs considerably in form among the various species. In certain American species the loops and angles are arranged exactly as in *M. (Arvicola) terrestris*, while in *M. przewalskii* and *M. luteus* the tooth, although retaining the same number of elements, is remarkably like that of some of the species of *Alticola*. (See Pl. XIII, Wissensch. Resultate der von N. M. Przewalski nach Cent.-Asien untern. Reisen. Zool. Theil, Bd. I, Lief. 3.) This resemblance to *Alticola* results from the unusual elongation of the posterior loop. In *Microtus lagurus* there are three tightly closed triangles, and the terminal loop has a well developed salient angle on each side at the base.

Other teeth.—In the Old World species (fig. 25) the back lower molar contains four tightly closed triangles. The American species, however (fig. 25), so far as known, have only three closed triangles in this tooth. The other molars are always formed as in tetramerodont *Microtus*. There is nothing peculiar about the incisors.

Mammæ.—In *Microtus pallidus*, or a closely related form, there are eight mammæ, four pectoral and four inguinal. I have been able to find no statement of the number of mammæ in the Asiatic species.

Feet.—Soles densely hairy as in *Phaiomys* and the lemmings; plantar tubercles, five; claws moderately developed, those on hind feet longest.

Fur.—The fur is full and soft, but not highly modified. In color most of the species are dull yellowish or grayish. The marking of *Microtus lagurus* is unique in the genus *Microtus* on account of the strongly developed and sharply defined dark dorsal streak.

General remarks.—The subgenus *Lagurus* is a strongly characterized group, but, as Dr. Merriam has remarked,¹ the species show no peculiarities to separate them generically from *Microtus arvalis*. In *Microtus lagurus*, *M. luteus*, and *M. przewalskii*, the tail is usually shorter than the hind foot, thus adding to the superficial resemblance to the lemmings. No other voles have the tail so short.

The subgenus *Lagurus* is represented in the Old World by *Microtus lagurus* (Pallas), *M. luteus* (Eversmann), and *M. przewalskii* (Büchner). In America there are probably numerous species and subspecies. Among these may be mentioned *Microtus pauperrimus* (Cooper), *M. curtatus* (Cope), and *M. pallidus* (Merriam).

¹ American Naturalist, XXIX, p. 758, August, 1895.

Subgenus ALTICOLA Blanford.

1884. *Alticola* Blanford, Journ. Asiat. Soc. Bengal, L, Pt. II, p. 89, 1884. Type *Arvicola stoliczkanus* Blanford.

Geographic distribution of type species.—"High plateaus of Northern Ladak (Western Tibet)" (Blanford).

Geographic distribution of subgenus.—Boreal Zone in the Himalayas.

Essential characters:

Palate abnormal.

m 3 without closed triangles.

m 1 with 4 or 5 closed triangles and 7 salient angles.

m 3 normally with 2 closed triangles and 5 or 6 salient angles; posterior loop produced backward in line of jaw.

Mammæ, 8.

Plantar tubercles, 6.

Sole, hairy.

Claws on hind feet longest.

Fur long and soft but not highly modified.

Skull.—The skull in this subgenus (Pl. I, fig. 10) shows no striking peculiarities to distinguish it from that of true *Microtus*. The general shape is usually much as in *Microtus arvalis*, but the zygomatic arches are more flaring and the brain case is somewhat broader and flatter. The rostrum is proportionally longer than in *Microtus* proper, and the audital bullæ (fig. 27) are more inflated and papyry.

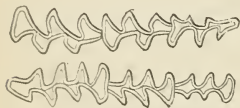


FIG. 26.—Enamel pattern of molar teeth, *Microtus* (*Alticola*) *albicauda* (type). (x 5.)

Bony palate.—The median palatal ridge (Pl. II, fig. 4) widens at a point opposite the space between the second and third molars and is approached, as in the typical microtine palate, by outgrowths from the opposite sides of the lateral grooves. These outgrowths, however, do not meet the median ridge, but leave the lateral grooves open. Just at its widest point the median ridge is squarely truncated. The sloping terminal ridge is entirely lacking and the space that it usually occupies forms the anterior end of the very long rectangular interpterygoid fossa. A structure of much the same appearance could be produced by widening the anterior end of such a hastate interpterygoid fossa as that often present in '*Aulacomys*' (Pl. II, fig. 7) until the whole space acquired an equal breadth. The floors and median walls of the lateral pits would then be so encroached upon as to obliterate the pits, while a few slight further modifications would give a palate indistinguishable from that of *Alticola*. The palate of *Alticola* resembles that of *Neofiber* more closely than it does that of any other subgenera except *Hyperacrius*.

Enamel pattern in general.—The enamel pattern in *Alticola* (fig. 26) differs in many ways from that of any subgenus of *Microtus*. In general it is characterized by (a) a tendency to reduction in the number of prisms in the variable teeth; (b) by a peculiar irregularity and indefiniteness in outline; (c) by a strong tendency toward bilateral symmetry

caused by the approximately equal size of the triangles on the opposite sides of the teeth, and (*d*) by the form of the posterior upper molar.

While the figures published by Blanford¹ in his paper on the voles of the Himalayas, Tibet, and Afghanistan are in many ways inaccurate, they give an excellent idea of the general appearance of the teeth in the voles of this group.

Front lower molar.—The first mandibular molar has normally four closed triangles and seven or eight salient angles. Rarely a fifth closed triangle is isolated at the inner basal angle of the anterior loop. The form, relative position, and degree of isolation of the triangles and transverse loops vary greatly with the different species. Any one of the reentrant enamel folds may fail to reach the enamel of the opposite side, and consequently any of the triangles may be open at one or both ends.

Back upper molar.—The posterior maxillary tooth varies in form in the different species. It is, however, always recognizable by the backward prolongation of the posterior loop in the line of the jaw, a character which is found elsewhere in *Hyperacrius*, *Chilotus*, and *Lagurus* only, and in all but the first of these developed to a much less degree. This attenuate posterior loop is followed by three or four more or less incompletely isolated lateral triangles, these by an anterior loop of the usual form. The tooth is most complex in *M. roylei* and *M. blanfordi*, in each of which it has six salient angles and two or three closed triangles.

Other teeth.—Except for the stronger tendency to bilateral symmetry combined with slight irregularity of outline the other molars do not differ from those of ordinary tetramerodont *Microtus*.

Mammæ.—The number of mammæ in the species of *Alticola* has apparently not been recorded. Blanford does not mention it in his descriptions of any of the species, and Mr. G. E. H. Barrett-Hamilton, who has made at my request a special examination of the material in the British Museum, is able to add nothing on the subject. In an adult nursing female of a species of *Alticola* closely allied to *Microtus albicauda* (No. 62162, U. S. Nat. Mus. Ladák side of Kara Korum Pass, Kashmir) there are eight well-developed mammæ. Hence there is little doubt that eight is the normal number in the subgenus.

Feet.—The feet are very hairy, the long hairs on the dorsal surface often nearly concealing the claws. Plantar tubercles six. The claws on all the feet are long and slender, those on the hind feet longer than those in front.

Fur.—As in most high boreal microtines the fur is long and full. Otherwise it is not peculiar.

General remarks.—The subgenus *Alticola* is one of the best characterized groups in the genus *Microtus*. The pattern of enamel folding is unlike that of any of the other subgenera, except *Hyperacrius*, while the palate structure is approached by that of *Hyperacrius* and the

¹ Journ. Asiatic Soc. Bengal, L, Pt. II, Pl. I, figs. B, C, D, and E.

otherwise widely different *Neofiber* only. The tendency to bilateral symmetry in the molars is shared by three other Asiatic subgenera, *Hyperacrius*, *Eothenomys*, and *Antelionmys*.

Alticola, like *Hyperacrius*, is apparently a strictly boreal subgenus. The following species are known: *Microtus stoliczkanus* Blanford, *M. roylli* (Gray), *M. stracheyi* (Thomas), *M. blanfordi* (Scully), and *M. albicauda* (True).

Subgenus HYPERACRIUS¹ Miller.

New subgenus. Type *Arricola fertilis* True.

Geographic distribution of type species.—"Central Kashmir, the Pir Panjal Range and the Kaj Nag Mountains." (True.)

Geographic distribution of subgenus.—Mountains of central and southwestern Kashmir at elevations ranging mostly from 7,000 to 12,000 feet.

Essential characters:

Palate abnormal.

m 3 without closed triangles.

m 1 normally with 4 or 5 closed triangles and 7 salient angles.

m 3 normally with 1 or 2 closed triangles and 4 salient angles.

Mammæ 4.

Plantar tubercles 5.

Sole hairy.

Claws on hind feet longest.

Fur short and dense.

Skull.—The skull in the subgenus *Hyperacrius* (Pl. I, fig. 11) differs from that of *Alticola* in its longer rostrum, strongly cuneate nasals, narrower interorbital constriction, more abruptly flaring zygomata, and

flatter brain case. The whole dorsal outline of the skull is depressed so that the zygomata are more nearly on the level with the top of the skull than in any other subgenus of *Microtus*. The auditory bullæ (fig. 27) are proportionally smaller than in *Alticola*, true *Microtus*, or *Pitymys*. The brain case is much more depressed



FIG. 27.—Auditory bullæ, (a) *Microtus (Alticola) albicauda*; (b) *M. (Hyperacrius) fertilis*. (x2.)

than in *Microtus* proper (flatter even than in *Pitymys*), and viewed from above it has a peculiar subcircular outline not known elsewhere in the genus. Parietals proportionally smaller than in *Microtus* proper; squamosals and interparietal proportionally larger. The latter in old individuals has much the same shape as in fully adult *Arricola*, *Neofiber*, and *Fiber*.

Bony palate.—The bony palate is exactly as in *Alticola*.

Enamel pattern in general.—The enamel pattern (fig. 28) has the general appearance of that of *Alticola*.

Front lower molar.—The first mandibular tooth is indistinguishable from the corresponding tooth in *Alticola*.

¹ Οι υπεράκριτοι, inhabitants of the heights.

Back upper molar.—The last maxillary tooth has the same general form as that of *Alticola*, but is simpler in structure, thus recalling the corresponding tooth in *Lagurus* (fig. 25). There are usually only two lateral triangles and four salient angles. The posterior loop is lengthened in the axis of the jaw as in *Alticola*.

Mammae.—There are four mammae, all inguinal.

Feet.—The feet are well haired, but rather less densely than in *Alticola*. Plantar tubercles five—the faintest possible trace of a sixth sometimes present. Claws on all four feet well developed, those on hind feet longest.

Fur.—The fur is much shorter and more dense than in *Alticola*.

Miscellaneous characters.—The ears, and apparently the eyes, also, are smaller than in *Alticola*. The whiskers are very short, reaching scarcely to the ears, while in *Alticola* they are probably longer than in any other subgenus of *Microtus*.

General remarks.—*Hyperacrius* is most closely related to *Alticola*, from which it differs chiefly in its highly modified skull and reduced number of footpads and mammae. Minor differences are to be found in the relative size of the ears and in the character of the feet. *Hyperacrius* appears to be modified for a more strictly underground life than *Alticola*. It requires no close comparison with any other subgenus, though it bears a superficial likeness both in external form and in cranial characters to *Pitymys*. The structure of the bony palate and the pattern of enamel folding readily distinguish it from the latter, however.

Whether *Microtus wynnei* may be associated with *Microtus fertilis* in the subgenus *Hyperacrius* is a matter of doubt. At my request Mr. G. E. H. Barrett-Hamilton has examined the specimens of *Alticola* in the British Museum with special reference to the relationships of *M. wynnei*. He finds that this species, as already noticed by Blanford, has only five plantar tubercles, but that in other characters it does not agree with the brief diagnosis of *Hyperacrius* that I sent him. The fur is long, as in the species of *Alticola*, and the skull apparently lacks the peculiar form seen in *Hyperacrius*. The number of mammae can not be determined in *M. wynnei* nor in any of the species of *Alticola* in the British Museum. For the present it is not safe to attempt to refer *Microtus wynnei* definitely to one subgenus or the other.

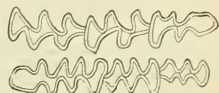


FIG. 28.—Enamel pattern of molar teeth, *Microtus* (*Hyperacrius*) *fertilis*. (x 5.)

Subgenus PEDOMYS Baird.

1857. *Pedomys* Baird, Mamm. N. A., p. 517, 1857. Type *Arvicola austerus* LeConte.

Geographic distribution of type species.—Transition and Upper Austral zones in the central United States and adjoining British Provinces.

Geographic distribution of subgenus.—The range of this subgenus is the same as that of *Microtus austerus*, the only known species.

Essential characters:

Palate normal.

m 3 without closed triangles.

m 1 normally with 3 closed triangles and 8 or 9 salient angles.

m 3 normally with 2 closed triangles and 6 salient angles.

Mammæ 4.

Plantar tubercles 5.

Sole thickly haired between heel and tubercles.

Claws moderate in length, those on hind foot longest.

Fur not specially modified.

Skull.—The skull of *Microtus austerus*, the only known species of *Pedomys*, is remarkable for the subcylindric brain case, and great depth of all that part back of the rostrum. While the skull of *Pedomys* is not strikingly different from that of true *Microtus*, it is very unlike the flattened skulls of *Phaiomys*, *Pitymys*, and *Chilotus*, the other groups of small voles resembling *Pedomys* in tooth characters and in number of mammae and footpads.

Bony palate.—The bony palate is typical, though the interpterygoid fossa is seldom squarely truncate anteriorly.

Enamel pattern in general.—The enamel pattern (fig. 29) is characterized by simplification in the structure of the variable teeth.

Front lower molar.—The first mandibular molar has a posterior transverse loop followed by three closed triangles and an anterior loop. The anterior loop is deeply indented by two reentrant angles, one on each side. These sometimes cut deep enough to isolate a fourth or even a fifth closed triangle, but this rarely takes place. There is often a very faintly developed reentrant angle close to each side of the tip of the anterior loop. In cases where these are strongly marked a front tooth precisely resembling that of *Microtus* is the result.

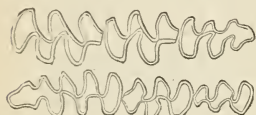


FIG. 29.—Enamel pattern of molar teeth, *Microtus (Pedomys) austerus*. (x 5.)

Back upper molar.—The posterior maxillary tooth is exactly like that of *Neofiber*, *Pitymys*, *Phaiomys*, *Chilotus*, and typical *Arvicola*, having an anterior transverse loop, two closed triangles and a short posterior loop, from the outer base of which a third closed triangle may sometimes be cut.

Other teeth.—With the exception of the two teeth just described, the dentition of *Pedomys* is like that of the tetramerodont species of the subgenus *Microtus*.

Mammæ.—There are four mammae, all inguinal.

Feet.—Soles densely hairy between heel and tubercles; pads five, with no indication of a rudimentary sixth.

General remarks.—*Pedomys* agrees in tooth pattern with *Pitymys*, *Chilotus*, and *Phaiomys*, but differs from all three in the shape of the skull, and from the last in the short claws and unmodified fur also.

Subgenus PHAIOMYS Blyth.

1863. *Phaiomys* Blyth, Journ. Asiat. Soc. Bengal, XXXII, p. 89, 1863. Type *Phaiomys leucurus* Blyth=*Microtus blythi* Blandford.

¹A skull of *Microtus ratliceps* from Norway exactly resembles skulls of *M. austerus* except that the rostrum is more slender.

1887. *Lasiopodomys* Lataste, *Annali del Mus. Civ. di Storia Naturale di Genova*, ser. 2a, Vol. IV, p. 268, 1887. Type *Arvicola branti* Radde.

Geographic distribution of type species.—"Banks of Tsho Morari and Pankong lakes, Western Tibet, also between Seh and the Pankong Lake at elevations above 13,000 feet." (Blanford.)

Geographic distribution of subgenus.—High plateau region of central and southern Asia. Probably does not occur below the Boreal zone.

Essential characters:

Palate normal.

m 3 without closed triangles.

m 1 normally with 3 to 5 closed triangles and 8 or 9 salient angles.

m 3 normally with 2 to 3 closed triangles and 6 salient angles.

Mammæ probably 10.

Plantar tubercles, 6.

Sole very hairy.

Claws very long and of about equal length on all four feet.

Fur remarkably long and soft.

Skull.—The skull of *Phaiomys* as compared with that of *Pedomys* is readily distinguished by its very different form. The brain case in *Pedomys* is high, long, and almost cylindrical, while that of *Phaiomys* is short, broad, and flat. The zygomatic arches are more broadly flaring in *Phaiomys* than in *Pedomys*, while the upper incisors are usually more prominent. The latter character is, however, inconstant.

Bony palate.—The bony palate is perfectly normal and requires no detailed description.

Enamel pattern in general.—The enamel pattern (fig. 30) is exactly like that of *Pedomys*, except that the outer reentrant angles in m 3 are somewhat less developed, while the anterior outer reentrant angle in m 2 usually divides the anterior loop into two closed triangles. These differences, however, are trivial and inconstant.

Other teeth.—In some of the members of the subgenus the incisors are directed more forward than usual. The character is, as already stated, wholly inconstant.

Mammæ.—There is still doubt as to the normal number of mammæ in the subgenus *Phaiomys*. Milne-Edwards found only four in a skin of *M. mandrianus*; Büchner found six in a skin of *M. strauchi*, and ten in a skin of *M. fuscus*. I am inclined to think that ten will prove to be the correct number.¹ In the specimen of *M. fuscus* just referred to there were six pectoral mammæ, the rest inguinal.

Feet.—The feet are large and densely haired. The number of tubercles on the sole is still a matter of doubt. Büchner records six in both

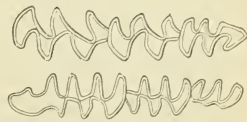


FIG. 30.—Enamel pattern of molar teeth, *Microtus (Phaiomys) strauchi*. (x 5.)

¹ That *Phaiomys* probably has a large number of mammæ—at least more than four—was suspected by Lataste, who in 1887 (*Annali del Museo Civico di Storia Naturale di Genova*, Serie 2a, Vol. IV, p. 270) called attention to the fact that Blyth found ten embryos in a female *Microtus blythi*.

M. brandti and *M. strauchi*, but I am able to find only five in a skin of the latter, even after thoroughly relaxing the foot. It is probable that six is the real number, as Büchner's determinations were made from alcoholic specimens. The claws on all four feet are large and about equal in length. That on the thumb is well developed—in this respect perhaps surpassing all other subgenera of *Microtus*.

Fur.—The fur is long and soft, suggesting that of a lemming rather than that of a vole.

General remarks.—In many respects *Phaiomys* resembles *Pedomys* so closely that I should hesitate to separate the two groups were they not already named. There are, however, such differences between them that it is impossible to call them the same, while in all probability more satisfactory material than that now available would show additional characters. In external appearance the two subgenera differ considerably. While *Pedomys* is a typical vole, *Phaiomys* bears a general resemblance to the lemmings. The peculiar aspect of the species of *Phaiomys* is caused by their short tails, large feet, and long, soft fur. The likeness between the species of *Phaiomys* and the yellowish species of the subgenus *Lagurus* is even more striking. From the latter, however, they are readily separable by dental characters.

Microtus blythi (Blanford), *M. mandarinus* (Milne-Edwards), *M. strauch*; Büchner, *M. fuscus* (Büchner), and *M. brandti* (Radde), are perhaps the best-known species of the subgenus *Phaiomys*.

Subgenus PITYMYS McMurtrie.

1830. *Psammomys* LeConte, Ann. Lyc. Nat. Hist., New York, III, p. 132, 1830 (genus).

Type *Psammomys pinetorum* Le Conte (not *Psammomys* Cretzschmar 1828).

1831. *Pitymys* McMurtrie, American edition, Cuvier Règne Animal, I, p. 434, 1831 (genus). Type *Psammomys pinetorum* LeConte.

1857. *Pitymys* Baird, Mamm. N. Am., p. 517, 1857 (section)

1887. *Pitymys* Lataste, Annali del Mus. Civ. di Storia Naturale di Genova, serie 2a, IV, p. 266, 1887 (subgenus).

1831. *Amomys* Bonaparte, Saggio Distrib. Metod. degli Anim. Vert., p. 20, footnote, 1831 (genus). Type *Psammomys pinetorum* Le Conte.

1836. *Pinemys* Lesson, Hist. Nat. d. Mamm. et Ois découv. depuis 1788, Compl. Oeuvres de Buffon, V, p. 436, 1836 (genus). Type *Psammomys pinetorum* LeConte.

1867. *Terricola* Fatio, Les Campagnols du Bassin du Léman, p. 36, 1867 (subgenus) (*subterraneus* and *savii*).

1876. *Micurus* Forsyth Major, Atti della Società Toscana di Sci. Nat., III, fasc. I, p. 126, 1876 (subgenus). Type *Arvicola nebrodensis* Mina Palumbo.

Geographic distribution of type species.—Austral Zone in the eastern United States.

Geographic distribution of subgenus.—Central and southern Europe, eastern United States, parts of Mexico.

Essential characters:

Palate, normal.

m 3 without closed triangles.

m 1 normally with 5 closed triangles and 9 salient angles.

in 3 normally with 2 or 3 closed triangles and 6 salient angles.

Mammæ, 4.

Plantar tubercles, 5.

Sole moderately hairy.

Claws on front feet longest.

Fur short, dense, and mole like.

Skull.—The skulls of the species of *Pitymys* differ considerably among themselves. In *Microtus pinetorum* (Pl. I, fig. 2), the most highly modified, the brain case is very broad and flat and the interorbital region is remarkably wide. The brain case is like that of *Lagurus*, but the broad anterior part of the skull is very different from the latter. The dorsal outline is strongly arched, especially anteriorly from the region between the orbits to the tips of the nasals. The arching is, however, no more strongly marked than in *Microtus arvalis*. In *Microtus subterraneus* the skull is like that of *M. pinetorum*, but the peculiarities are less accentuated. In the Mexican species of *Pitymys* the brain case is narrower and higher than in *M. pinetorum*, and the anterior part of the skull is less heavily built. The zygomatic processes of the maxilla stand out more nearly at right angles with the side of the skull, thus bringing the broadest part of the zygomatic arch farther forward than in *M. pinetorum*.

Bony palate.—The palate is normal, though the region between the posterior molars is in *M. pinetorum* rather flatter than usual in true *Microtus*, and the anterior outline of the interpterygoid fossa is often somewhat hastate.

Enamel pattern in general.—With the exception of the front lower molar and back upper molar, the enamel pattern (fig. 31) is that of tetramerodont *Microtus*.

Front lower molar.—The anterior mandibular tooth contains the same number of loops and angles as the corresponding tooth in *Microtus arvalis*. As a rule, however, the first and second triangles are not completely isolated from each other or from the anterior loop. The tooth is therefore exactly as in *Pedomys*.

Back upper molar.—The posterior maxillary tooth is simplest in the American species of the subgenus. In these it is like the back upper tooth in *Pedomys* and *Arvicola*, which contain two closed triangles and an anterior and posterior loop. In *M. subterraneus*, however, the tooth is formed exactly as in *M. arvalis*, while in *M. savii* it is somewhat intermediate. In the last-named species the terminal loop is slightly larger than in *M. pinetorum*, and a third closed triangle is usually cut off from the outer base.

Other teeth.—There is nothing peculiar about the incisors or remaining molars.

Mammæ.—In *Pitymys* there are only four mammæ—all inguinal.

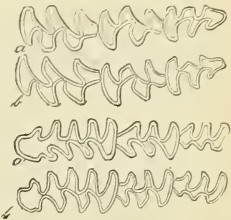


FIG. 31.—Enamel pattern of molar teeth, (a) *Microtus (Pitymys) pinetorum*; (b) *M. (P.) savii*. (x 5.)

Feet.—The soles are moderately hairy. They have five well-developed tubercles, but no trace of a sixth. The claws are well developed on all the feet, those on the front feet either equaling or exceeding those on the hind feet.

In *M. pinetorum* the front feet are much larger and the front legs shorter than in true *Microtus*. These peculiarities are less developed in *M. subterraneus* and *M. savii*. Of the other species I have not seen alcoholic specimens, and so am unable to say which of those mentioned they most closely resemble.

Fur.—The fur in all the known species is remarkably short and dense. This character is most noticeable in *M. pinetorum*, which has an almost mole-like coat.

Miscellaneous characters.—The tail, eyes, and external ears are much reduced in all the species of *Pitymys*. These characters, as well as the peculiarities of the fur and front feet, are distinctly adaptive and fit the animals for their underground life.

General remarks.—While *Pitymys* agrees with *Pedomys* in the number of mammae and footpads, it is readily distinguished by its highly modified fur, small eyes and ears, and flattened skull. The type and most extremely developed species is further characterized by its greatly shortened front legs.

Pitymys is represented in America by *Microtus pinetorum* (Le Conte) and several forms related to *M. quasiater* (Coues). In Europe a number of species and subspecies occur. Among these the best known are *M. subterraneus* (De Selys Longchamps) and *M. savii* (De Selys Longchamps).

Subgenus CHILOTUS Baird.

1857. *Chilotus* Baird, Mamm. N. Am., p. 516, 1857. Type, *Arvicola oregoni* Bachman.

Geographic distribution of type species.—Oregon, Washington, and British Columbia.

Geographic distribution of subgenus.—The range of the subgenus *Chilotus* is coincident with that of the type and only known species.

Essential characters:

Palate normal.

m 3 normally without closed triangles.

m̄ 1 with 5 closed triangles and 9 or 10 salient angles.

m 3 with 2 or 3 closed triangles and 6 salient angles.

Mammae 8.

Plantar tubercles 5.

Sole moderately hairy.

Claws on hind feet longest.

Fur short and dense.

Skull.—The skull of *Chilotus* (Pl. I, fig. 8) is low and flat, the dorsal outline nearly straight, and the brain case not widened, as in *Pedomys*. As compared with *Pedomys*, the rostrum is remarkably long and slender in proportion to the rest of the skull.

Bony palate.—The palate is normal and calls for no further remark.

Enamel pattern in general.—The enamel folding (fig. 32) is like that of the tetramerodont species of *Microtus*, except that the back upper tooth is a little simplified.

Front lower molar.—The first mandibular molar is exactly like that of typical *Microtus*.

Back upper molar.—The back maxillary tooth contains a transverse anterior loop, two lateral closed triangles, and a somewhat lengthened terminal loop. The latter has at each side of its base a conspicuous angle, the outer one of which is often isolated as a third closed triangle. The tooth has six salient angles, two to each of the transverse loops and one to each of the closed triangles.

Other teeth.—As already stated, the remaining teeth are formed exactly as in tetramerodont *Microtus*. One specimen from British Columbia has the lateral triangles closed in the back lower molar.

Mammae.—There are eight mammae, four pectoral and four inguinal.

Feet.—Soles moderately hairy from heel to tubercles; plantar tubercles five, all well developed; claws on hind feet longest; front feet not modified like those of typical *Pitymys*.

Fur.—The fur is shorter and more dense than in true *Microtus*, but the modification is not carried so far as in *Microtus (Pitymys) pinetorum*.

General remarks.—*Chilotus* combines the mammae and foot pads of *Arvicola* with the nearly typical enamel pattern of *Microtus* and has a form of skull peculiarly its own. In general it is modified in the same direction as *Pitymys*, but to a much less degree.

Great stress has been laid on the form of the ear as a character of this subgenus. In the original description¹ Baird says:

A specimen in alcohol, from Steilacoom, received since the preceding description was prepared, is, in size, much as described. The ears are low, orbicular, the membrane thickened, the margins or conchal portion much inflected or incurved, like a half-open apple blossom, the concha being inflected all round. The antitragus is well developed, but rather low. The surfaces of the ear appear perfectly naked, with, however, a ciliation of long hairs toward the roots of the concha, on the dorsal surface. A close examination of the auricle in the dried specimen shows a few scattered, very short, white hairs.

The structure of the ear, though in many respects similar to that of *A. pinetorum*, is yet essentially different. Thus the upper and lower roots of the margin of the ear meet anteriorly so as to form even a low rim to the meatus anteriorly, completely inclosing the aperture; the edge of the concha is inflected; the region inside the auricle, around the meatus, naked, and the antitragus so much developed as to be capable of completely closing the meatus. In *A. pinetorum* the roots of the upper and lower margins of the ear are widely separated, by a space of a quarter of an inch, the space between these roots and anterior to the meatus perfectly plane; the edges of the concha, or of the auricle, not inflected at all; the inner space around the meatus partly hairy; the antitragus very slightly developed, not valvular, nor capable of closing the meatus at all.

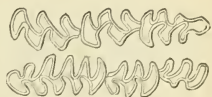


FIG. 32.—Enamel pattern of molar teeth, *Microtus (Chilotus) oregoni*. (x5.)

¹ Mamm. N. Am., p. 538, 1857.

Through Mr. True's kindness I have been able to examine one of the alcoholic specimens on which Baird based this description. This specimen (No. 2533, from Tomales Bay, Cal.¹) is in good condition and shows most of the peculiarities to which attention was called. The thickening of the edge of the annicle is, however, due to disease or to the action of the parasites which often attack the rims of the ears in the voles and other small rodents. The anterior base of the ear is not essentially different from the same region in *Pitymys*, though the valvular fold is slightly more developed. It is probable that by means of this fold the meatus in *Pitymys*, as well as in most if not all of the voles, can be tightly closed.

Subgenus MICROTUS Schrank.

1798. *Microtus* Schrank, Fauna Boica, I, 1ste Abth., p. 72, 1798. Type by elimination *Microtus terrestris* Schrank = *Mus arvalis* Pall.
 1817. *Mynomes* Rafinesque, Am. Monthly Magazine, II, p. 45, 1817. Type *Mynomes pratensis* Raf. = *Arvicola pennsylvanicus* Ord.
 1836. *Hemiotomys* DeScl'ys Longchamps, Essai Monographique sur les Campagnols des environs de Liège, p. 7, 1836, part (included *arvalis* and *terrestris*).
 1857. *Hemiotomys* Baird, Mamm. N. Am., p. 515, 1857.
 1849. *Neodon* Hodgson, Ann. and Mag. Nat. Hist., 2d ser., III, p. 203, 1849. Type *Neodon sikkimensis* Hodgson.
 1857. *Paludicola* Blasius, Fauna der Wirbelthiere Deutschlands, I, p. 333, 1857, part (included *terrestris*, *nivalis*, and *ratticeps*).
 1857. *Agricola* Blasius, Fauna der Wirbelthiere Deutschlands, I, p. 334, 1857. Type *Arvicola agrestis*.
 1867. *Praticola* Fatio, Les Campagnols du Bassin du Léman, p. 36, 1867, part (included *terrestris*, *nivalis*, *arvalis*, *ratticeps*, and *campestris*).
 1867. *Sylvicola* Fatio, Les Campagnols du Bassin du Léman, p. 63, 1867. Type *Arvicola agrestis*.
 1890. *Campicola* Schulze, Schriften Naturwiss. Vereins d. Harzes in Wernigerode, V, p. 24, 1890, part (included *arvalis*, *subterraneus*, and *campestris*).
 1894. *Tetramerodon* Rhoads, Proc. Acad. Nat. Sci. Phila., p. 282, 1894. Type *Arvicola tetramerus* Rhoads.

Geographic distribution of type species.—Central Europe.

Geographic distribution of subgenus.—Boreal region of both hemispheres, south to Mexico, northern India, and southern Europe.

Essential characters:

Palate normal.

m 3 without closed triangles.

m 1 normally with 5 closed triangles and 9 salient angles.

m 3 normally with 3 closed triangles and 7 or 8 salient angles.

Mammae, 8.

Plantar tubercles, 6.

Sole moderately hairy.

Claws of hind feet longest.

Fur not specially modified.

Skull.—In true *Microtus* (Pl. I, fig. 3) the skull lacks the peculiar modifications found in such subgenera as *Lagurus*, *Pitymys*, *Chilotus*,

¹ No. 2529 from Steilacoom, Wash., also mentioned by Baird, is lost.

and others. Within certain limits, however, the skull varies considerably in size and form, so that it is difficult to frame any accurate diagnosis. The skull of *Microtus arvalis* figured on Plate I represents the form characteristic of the great majority of species. One of the most notable departures from this type is seen in the skull of *Microtus nivalis*, which has an unusually low, broad brain case, and flat dorsal outline.

Bony palate.—The bony palate in the subgenus *Microtus* (fig. 7 A, and Pl. II, fig. 5) shows in its most perfect development the form which may be considered the normal one in the genus, since it is characteristic of most of the subgenera and of the vast majority of species. As this palate has already been described (pp. 26–27) it is necessary here to notice a few departures from the type form only. In young individuals the sloping ridge is broader than in the adults, while in very old individuals it often becomes very abrupt and at the same time greatly narrowed. These two extremes, which are usually characteristic of immaturity and old age, occur as the normal condition in the adults of certain species. In *Microtus nivalis* the ridge is broad and flat, while in *M. agrestis*, *M. ratticeps*, and most of the American species it is narrow and abrupt. Occasionally (especially in *M. agrestis* and *M. ratticeps*) the anterior edge of the interpterygoid fossa is encroached upon by the projecting median ridge. The latter, on

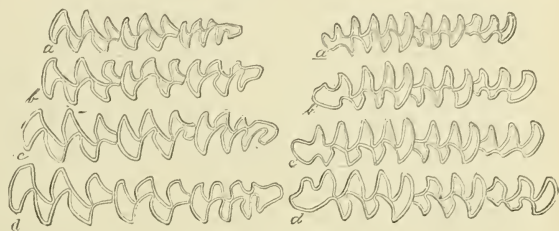


FIG. 33.—Enamel pattern of molar teeth, (a) *Microtus* (*Microtus*) *arvalis*; (b) *M. (M.) nivalis*; (c) *M. (M.) pennsylvanicus*; (d) *M. (M.) ratticeps*. (x 5.)

the other hand, may be slightly cleft in the median line, thus foreshadowing the first step in the series of changes which lead to the very different palate of *Erotomys*.

Enamel pattern in general.—The enamel pattern in the subgenus *Microtus* (fig. 33) is characterized by the large number of loops and angles in the first lower molar and last upper molar.

Front lower molar.—The first lower molar normally contains a posterior transverse loop, five closed triangles, two of which are on the outer side and three on the inner side, and finally an anterior loop which is usually more or less deeply cut by two reentrant angles, one on each side of the loop, the outer of which is always the more posterior of the two. With these loops and triangles are usually associated nine well-developed salient angles, two formed by the posterior transverse loop, one by each of the five closed triangles, and one by each side of the base of the anterior loop. That part of the anterior loop which lies in front of the reentrant angles may develop a salient angle on its inner side, less frequently one on the outer side. Very rarely the loop may be cut by a third reentrant angle. This condition occurs in adult spec-

imens of *Microtus agrestis*, *M. pennsylvanicus*, also in the type of *M. (Arvicola) arvicoloides* (fig. 35), and probably in many other species with the tooth formed after the pattern of *Microtus arvalis*. The other variations in the form of the front lower molar are the result of the greater or less development of the reentrant angles normally present at the anterior end. Sometimes the fourth reentrant angle (counting from behind) on the lingual side of the tooth fails to meet the third on the opposite side. Very rarely the anterior outer triangle opens in a like manner into the anterior inner triangle, and the latter at the same time communicates with the anterior loop, thus producing a tooth like that normally present in *Pedomys* and *Pitymys*. Rather frequently a sixth closed triangle is cut off from the outer basal corner of the anterior loop, and occasionally a seventh triangle is isolated at the inner side of the greatly reduced loop.

The variations just described are purely individual and occur in the species having the tooth of the typical form. Two notable variations from this form are normally found in *Microtus ratticeps* and *M. nivalis*. In the former (fig. 33*d*) the fifth triangle opens into the short, unindented anterior loop. There is here an actual reduction in the elements of the tooth, which has only eight salient angles, thus resembling the corresponding tooth in *Pedomys*. In *M. nivalis* (fig. 33*b*), while there are five closed triangles and nine salient angles, the anterior loop is small and crescentic, much resembling the posterior loop in the maxillary teeth of *Eothenomys*.

Back upper molar.—The last upper molar is normally made up as follows: An anterior transverse loop, succeeded by three closed triangles, two smaller ones on the outer side and a larger one on the inner side, these in turn by a posterior loop of variable shape. The tooth usually contains seven salient angles, two to each of the transverse loops and one to each of the three closed triangles.

Variations in the form of this tooth are numerous. Beginning at the anterior end where the structure is most definite, it is found that the first outer triangle very frequently opens into the large inner triangle, less often into the anterior loop. The second outer triangle very rarely opens into the inner triangle, but is rather frequently in communication with the posterior loop. The posterior loop varies in form and size, the variations being partly individual and partly characteristic of species. For the present it is unnecessary to discriminate in all cases between the two categories. The most usual form and that found in the type species, *Microtus arvalis* (fig. 33*a*) is an irregular crescent with the concavity directed inward and backward and the posterior tip thickened, the whole joined to the rest of the tooth at a point on the convexity midway between the middle and the anterior extremity. This nearly crescentic form is usually distorted by the elongation and straightening of the anterior limb, so that the resulting shape is more like that of the letter J. The thickened posterior extremity of the loop is often

extended and cut by a reentrant angle on the lingual side, so that the crescent is modified into the form of a rude E. Occasionally the anterior extremity of the crescent is isolated as a second inner triangle. The convex side of the crescent may develop a more or less prominent salient angle. This condition is normal in *Microtus ratticeps* and *Microtus chrotorrhinus*, but occurs also in other species. In the aberrant *Microtus nivalis* the structure of this tooth is simplified so that it is essentially as in *Arvicola*, *Pedomys*, and *Pitymys*.

Other teeth.—The first and second upper molars contain each an anterior transverse loop and, respectively, three and two closed triangles. In *Microtus agrestis*, *M. sikkimensis*, *M. pennsylvanicus*, *M. terranova*, and *M. aztecus* the inner edge of *m*2 is produced into a conspicuous loop, which frequently becomes isolated, so as to form a closed triangle about half the size of the others. The European species with *m*2 formed in this way have been placed in a subgenus called *Agricola* or *Sylvicola*, while the American species have been referred to *Mynomes* in a restricted sense. The American species with *m*2 exactly as in *Microtus arvalis* have received the name *Tetramerodon*. While the name *Tetramerodon* can not be used in a subgeneric sense, it is frequently convenient to speak of the voles with the enamel pattern of *M. arvalis* as the tetramerodont species to distinguish them from their pentamerodont allies. In *Microtus sikkimensis* a supplemental triangle is developed in *m*1 as well as in *m*2. On account of this peculiarity the animal has been made the type of the genus or subgenus 'Neodon.' Neither *Neodon* nor *Agricola* are worthy of recognition as subgenera distinct from *Microtus*. Their characters are of trifling importance, while in other species of *Microtus* (as, for instance, *M. nivalis*, *M. guentheri*, and occasionally *M. pennsylvanicus*) intermediate conditions can be found.

Mammæ.—In the subgenus *Microtus* the mammæ are always eight, four pectoral and four inguinal. No exceptions to this number are known.

Feet.—There are six tubercles on the sole. Five of these are always well developed, but the sixth is variable in size, being especially large in *M. ratticeps*. The sole is always moderately hairy from heel to tubercles. It is never densely furred as in *Phaiomys* or naked as in *Neofiber*. The claws on all four feet are moderately developed, those on the hind feet always slightly larger than those on the front feet, the latter never specially developed for digging (cf. *Pitymys*).

Fur.—The fur is moderately full and soft, neither long and silky as in *Phaiomys* nor dense and mole-like as in *Pitymys*.

General remarks.—The subgenus *Microtus* needs comparison with the groups having normal or very slightly abnormal palates: *Arvicola*, *Pedomys*, *Pitymys*, *Chilotus*, *Phaiomys*, and *Lagurus*. From all the others it differs too widely to give rise to confusion. *Lagurus* is distinguished from *Microtus* by the tightly closed triangles in the posterior

mandibular tooth, *Arvicola* by the presence of large musk glands on the sides, *Pedomys* and *Pitymys* by reduction in the numbers of both mammae and plantar tubercles, *Chilotus* by reduction in the latter only, and *Phaiomys* by an increase in the number of mammae and by the very large claws. More extended comparisons will be found under each of these subgenera.

This subgenus is the most widely and generally distributed, as well as the one containing the largest number of species. Although the species of *Microtinae* are still very imperfectly known, there is little doubt that the members of the subgenus *Microtus* greatly outnumber the species of all the other genera and subgenera together. Conspicuous representatives of the subgenus *Microtus* are (in the Old World): *Microtus arvalis* (Pall.), *M. agrestis* (Pall.), *M. ratticeps* (Keys. & Blas.), *M. nivalis* (Martins), *M. guentheri* (Dansford & Alston), *M. sikkimensis* (Hodgson); (in America): *Microtus pennsylvanicus* (Ord), *M. terranovæ* (Bangs), *M. xanthognathus* (Leach), *M. chrotorrhinus* (Miller), *M. longicauda* (Merriam), *M. mogollonensis* (Mearns), *M. townsendi* (Bachman).

Subgenus ARVICOLA Lacépède.

1801. *Arvicola* Lacépède, Mém. de l'Institut, Paris, III, p. 489, 1801 (genus). Type, '*Arvicola amphibius*' = *Mus terrestris* Linn.
 1883. *Arvicola* Lataste, Le Naturaliste, Tome II, p. 349, 1883 (subgenus).
 1836. *Hemiotomys* De Selys Longchamps, Essai Monographique sur les Campagnols des environs de Liège, p. 7, 1836, part (included *arvalis* and *terrestris*).
 1857. *Paludicola* Blasius, Fauna der Wirbelthiere Deutschlands, I, p. 333, 1857, part (included *terrestris*, *nivalis*, and *ratticeps*).
 1867. *Ochetomys* Fitzinger, Sitzungsber. K. Akad. Wiss. Wien, LVI, p. 47, 1867. (No type mentioned, but genus intended to include all the water rats of Europe.)
 1867. *Praticola* Fatio, Les Campagnols du Bassin du Léman, p. 36, 1867, part (included *terrestris*, *nivalis*, *arvalis*, *ratticeps*, and *campestris*).
 1894. *Aulacomys* Rhoads, American Naturalist, XXVIII, p. 182, 1894. Type, *Aulacomys arvicoloïdes* Rhoads.

Geographic distribution of type species.—Northern Europe.

Geographic distribution of subgenus.—Northern part of Northern Hemisphere, exclusive of America east of the Rocky Mountains.

Essential characters:

Palate slightly abnormal.

m 3 occasionally with closed triangles.

m 1 normally with 3 to 5 closed triangles and 7 to 9 salient angles.

m 3 normally with 2 or 3 closed triangles and 6 to 8 salient angles.

Mammæ 8.

Plantar tubercles 5.

Sole almost naked.

Claws on hind feet longest.

Fur slightly modified.

Musk glands present on sides of body.

Skull.—The skull of the larger Old World species of *Arvicola* (Pl. I, fig. 9) is nearly as large as that of *Neofiber*. In the American species

(Pl. I, fig. 1) it is smaller, though considerably larger than in most species of *Microtus* proper. Aside from its large size and prominent ridges, the skull of *Arvicola* differs from that of *Microtus* in its broader, shorter brain case, more widely flaring zygomatic arches, and proportionally slender rostrum. The peculiar appearance of the rostrum is heightened by the fact that the incisors project more than usual. Some of these characters are more noticeable in the American species, though the latter show no cranial peculiarities of sufficient importance to separate them subgenerically from those of the Old World. In the American species the skull is usually more lightly built and less strongly angular than in the typical members of the genus (compare figs. 1 and 9 of Pl. I).

Bony palate.—The bony palate is usually normal, but occasionally the median sloping ridge is divided in the median line, so that the interpterygoid fossa is hastate anteriorly (Pl. III, fig. 7). This condition occurs most frequently in the American species, but even among these it is inconstant.

Enamel pattern in general.—The enamel pattern in typical *Arvicola* (fig. 34*b*) is characterized by the great reduction in the number of closed triangles and salient angles in the front lower molar and back upper molar. In these peculiarities, though closely approached by *Pitymys*, *Pedomys*, and *Phaiomys*, it presents the extreme conditions found in the genus. The third lower molar shows the tendency to closure of the lateral triangles characteristic of all the larger members of the genus. The pattern of enamel folding in the molar teeth of the American species of *Arvicola* (fig. 34*a*) is, on the other hand, exactly like that of the tetramerodont species of the subgenus *Microtus* (e. g., *Microtus arvalis* and most of the western American species).

Front lower molar.—In the typical species the simplification in the structure of the teeth is carried furthest in the first lower molar. This tooth normally contains a posterior transverse loop followed by three closed triangles (one on the outer side, two on the inner side) and a terminal transverse loop which is deeply constricted in the middle. Each transverse loop forms two salient angles and each lateral triangle one, making seven in all. Deviations from this form are very rare. In one or two specimens I have seen a fourth triangle isolated on the outer side, thus producing a tooth much like the corresponding one in *Microtus* (*Microtus*) *ratticeps*, a species which has the last upper molar very complicated in structure. The front lower molar in typical *Arvicola* differs from that of the other groups in which it has only three closed triangles in the reduced number of salient angles—seven instead of

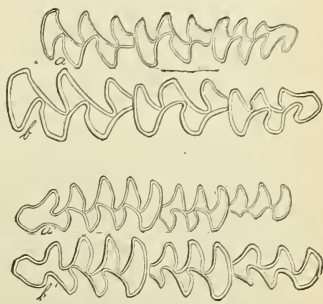


FIG. 34.—Enamel pattern of molar teeth,
(a) *Microtus* (*Arvicola*) *macropus*;
(b) *M. (A.) terrestris*. (x5.)

nine. Since this tooth in the American species has the same structure as in *Microtus arvalis*, no special description is necessary.

Back upper molar.—In the typical species the last upper molar has an anterior transverse loop, a closed triangle on each side, and a very short, simple terminal loop. With these loops are associated six salient angles, two on each of the terminal loops and one on each closed triangle. Rarely the posterior terminal loop is reduced by the isolation of the outer basal angle as a third closed triangle, but this seldom happens, while the resulting form of tooth is quite different from that found in any member of the subgenus *Microtus* except the aberrant *M. nivalis*. In the American species this tooth is formed exactly as in *Microtus arvalis*.

Mammæ.—There are eight mammæ in *Arvicola*, as in *Microtus*.

Feet.—In *Arvicola* the soles are very sparsely haired or almost naked between the tubercles and the heel.

The tubercles are only five in number, as the small one which in *Microtus* lies midway between the large proximal tubercle and the base of the fifth toe is absent. Claws moderately developed, those on hind feet slightly the larger.

Fur.—The fur is close, dense, and long, the under fur especially thick and woolly. It thus resembles the fur of *Neofiber*, though the modification is not carried so far as in the latter.

Miscellaneous characters.—The species of *Arvicola* are provided with a large musk gland on each side of the abdomen. These glands lie immediately in front of the hind legs and are very conspicuous in alcoholic specimens. In a half-grown male *Microtus terrestris* from St. Petersburg, Russia, each gland is 13 mm. long by 6 mm. wide. They are regularly oval in outline, the long axis parallel with the long axis of the body. The surface, which is slightly raised above that of the surrounding skin, is closely and irregularly wrinkled, and has much the appearance of very finely honeycombed tripe. Each gland bears a sprinkling of fine hairs much shorter than the fur, but at first sight appears to be naked. In dried skins the positions of the glands are indicated by tufts of grease-soaked fur.

General remarks.—The subgenus *Arvicola* is distinguished from all other groups with similar enamel pattern or with like numbers of mammæ and foot pads by the presence of the large glandular masses on the sides of the body. The species are all water rats, and, with the exception of *Microtus (Neofiber) alleni*, they considerably exceed the other members of the genus in size.

Although this subgenus is now for the first time recorded from America, at least three species of *Arvicola* inhabiting the western United States have been described within the past five years. These are *Microtus macropus* (Merriam), *M. arvicoloides* (Rhoads), and *M. principalis* Rhoads. *Microtus macropus* was supposed to be "one of the western members of the subgenus or section *Mynomes*," that is, a tetramerodont *Microtus*.¹ *Microtus arvicoloides* was made by its descri-

¹North American Fauna No. 5, p. 60, July, 1891.

ber the type of a new genus, *Aulacomys*,¹ while *M. principalis*, closely allied to both *M. macropus* and *M. arvicoloides*, was referred by the same author to true *Microtus*.² This confusion arose from the fact that the subgeneric and generic determinations were based chiefly on dental characters. Hence *Microtus macropus* and *M. principalis* were naturally considered members of the subgenus *Microtus*, since both have the enamel pattern characteristic of the tetramerodont species of that group.

The teeth of the type and only known specimen of *Microtus arvicoloides*, on the other hand, show certain characters which, although clearly abnormal, led to an entire misunderstanding of the animal's true relationships. The first of these abnormal characters, and the one which suggested the name *Aulacomys*, is seen in the upper incisors. Each of these has a narrow longitudinal median groove. They can not, however, be considered as entitling the species to generic rank, since similar though fainter grooves are occasionally found in almost any species of *Microtus*, while they are absent in the vast majority of specimens of '*Aulacomys*.' The second abnormality in the type of *Microtus arvicoloides* is in the form of the front lower molar. This tooth (fig. 35) has two reentrant angles on the outer side of the anterior loop instead of one as usual in *Microtus*. The supplemental reentrant angle, like the grooves in the incisors, is purely an individual character, which may crop out in any species of *Microtus*, with the front lower molar formed as in *M. arvalis*, and which is absent in all the other thirty or more specimens of '*Aulacomys*' that I have seen. The subgenus *Aulacomys* if retained as distinct from *Arvicola* must rest on characters of enamel pattern alone, since in all other peculiarities it agrees perfectly with the latter. The differences in enamel folds are rather considerable, since '*Aulacomys*' has the highly complicated pattern of true *Microtus*, while the species of typical *Arvicola* have the simplest pattern of any known. While it seems highly inadvisable to base subgeneric divisions on such characters, the decision rests on purely individual judgment.

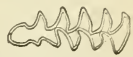


FIG. 35.—Abnormal front lower molar of type specimen of '*Aulacomys arvicoloides*. (x4.)

In the Old World numerous species and subspecies are probably confused under the name '*Arvicola amphibius*.' *Microtus musignani* (De Selys Longchamps) and *M. monticola* (De Selys Longchamps) appear to be especially distinct from *M. terrestris* (Linn.).

Subgenus NEOFIBER True.

1884. *Neofiber* True, Science, IV, p. 34, July 11, 1884 (full genus). . Type *Neofiber alleni* True.

1891. *Neofiber* Merriam, North American Fauna, No. 5, p. 59, July, 1891 (subgenus).

Geographical distribution of type species.—Florida. "Doubtless a common animal in favorable localities throughout the State." (Chapman.)

¹American Naturalist, XXVIII, p. 182, February, 1894.

²American Naturalist, XXIX, p. 940, October, 1895.

Geographical distribution of subgenus.—The range of the subgenus *Neofiber* is the same as that of the type and only known species.

Essential characters:

- Palate abnormal.
- m 3 with all triangles closed.
- m 1 with 5 closed triangles and 9 salient angles.
- m 3 with 2 closed triangles and 6 salient angles.
- Mammæ 4.
- Plantar tubercles 5.
- Sole naked.
- Claws on hind feet longest.
- Fur highly modified.

Skull.—The skull of *Neofiber* is characterized by its large size, great depth through the frontal region, and conspicuous development of postorbital processes. The ratio of fronto-palatal depth to basilar length is about 41 in *Neofiber*, while in true *Microtus* it is only about 35. As the occiput in *Neofiber* is not correspondingly high the dorsal outline of the skull curves gently and regularly from front to back, with the highest point just behind the orbits. When viewed from above the skull of *Neofiber* differs from that of *Microtus* chiefly in the larger squamosals, smaller parietals and interparietal, and in the sharp-pointed postorbital processes. The latter project over the orbital cavity as square-cornered shelves, which are especially noticeable when viewed from below.

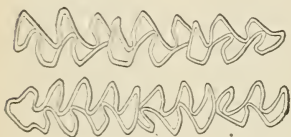


FIG. 36.—Enamel pattern of molar teeth, *Microtus (Neofiber) alleni*. (x 4.)

Palate.—The bony palate in *Neofiber* (Pl. II, fig. 9) differs widely from that of *Microtus*, and exactly resembles that of *Fiber* (p. 72).

Enamel pattern in general.—In general the enamel pattern of *Neofiber* (fig. 36) is characterized by a tendency to reduction in the number of angles in the variable teeth and to the tight closure of all triangles. The latter peculiarity gives the teeth the greatest possible strength.

Front lower molar.—The first molar in the lower jaw exactly resembles the corresponding tooth in *Microtus* except that the anterior loop is rather shorter than in the typical members of that subgenus. In one specimen (No. 23453, U. S. Nat. Mus.) the anterior loop has two indentations on the outer side, thus suggesting *Anaptogonia*.

Back upper molar.—The third maxillary tooth is like that in the subgenera *Pitymys*, *Pedomys*, *Phaiomys*, *Chilotus*, and typical *Arvicola*, as it has only two closed triangles and six salient angles.

Other teeth.—The back lower molar has all the triangles tightly closed, in this respect differing from all other subgenera except *Lagurus*. Closed triangles are sometimes formed in the third lower molar of almost any of the larger voles, but *Neofiber* and *Lagurus* are the only groups in which they are always present. Outside the subgenus *Lagurus*, most of the known species of which are small, the tendency to

closure of the triangles in this tooth increases with the size of the animals until in such large species as *Microtus alleni* and the members of the genus *Fiber* they are always tightly closed. *Microtus terrestris*, the only species approaching *M. alleni* in size, has closed triangles in $m3$ very often, while in one specimen the tooth is formed exactly as in *Neofiber*. *M. principalis* Rhoads, another large species, also rather frequently shows closed triangles in this tooth. The incisors, like those of *Fiber*, are short, broad, and very strong, in this respect reaching the opposite extreme from that attained by '*Aulacomys*.'

Mammæ.—Apparently the number of mammæ in *Neofiber* has never been stated in print. Mr. Outram Bangs writes me, however, that he found four inguinal teats in an adult female *Microtus alleni* which he took in Brevard County, Fla., during February, 1895.

Feet.—Soles wholly naked, foot pads five, as in *Arvicola*; claws on hind feet longest.

Fur.—The fur is modified to meet the requirements of an aquatic life in the same way and to almost the same extent as in the genus *Fiber*. The under fur is exceedingly thick, woolly, and dense, while the longer hairs are very glossy and lustrous. This condition is suggested in *Arvicola*, where, however, the modification is not carried so far.

Miscellaneous characters.—Whether *Neofiber* is provided with mask glands like those of the other water rats is at present uncertain. Collectors have failed to notice them, but they might easily escape detection in the thick fur unless specially searched for. The only alcoholic specimen that I have examined is not full grown. This shows no trace of the glands even when the skin of the sides is raised and examined from beneath.

General remarks.—In *Neofiber* are combined the mandibular enamel pattern of *Lagurus* with the maxillary enamel pattern and external characters of typical *Arvicola*, complicated by a reduction in the number of mammæ as in *Pedomys* and *Pitymys*.

Genus FIBER Cuvier.

Fiber Cuvier [Tabl. Élé. de l'Hist. Nat. des Anim., p. 141, 1798], Leçons d'Anat. Comp., I, tabl. I, 1800. Type *Castor zibethicus* Linn.

Geographic distribution of type species.—North America north of the southern border of the United States.

Geographic distribution of genus.—The range of the genus *Fiber* is essentially the same as that given for the type species.

Essential characters:

Upper incisors with anterior faces smooth.

Lower incisors with roots on outer side of molars.

Molars rooted.

Enamel pattern characterized by approximate equality of reentrant angles on outer and inner sides of molars.

Feet modified for swimming.

Tail flattened laterally.

Skull.—The skull (fig. 37) differs very slightly from that of *Microtus* except that it is considerably larger than in any known species of the latter, and has a proportionally longer rostrum. The bony palate (Pl. II, fig. 12) resembles that of the species of *Alticola* and *Neofiber* in the extension forward of the interpterygoid fossa and suppression of the sloping part of the median ridge. The posterior border is thus squarely cut off immediately behind the lateral bridges. A vestige of the sloping ridge usually persists in the form of a median spine projecting into the interpterygoid space. The skull of *Fiber* is peculiar in the expansion of the squamosals on the dorsal surface of the skull at the expense of the parietals. The postorbital processes of the squamosals form prominent triangular projections closely resembling those of *Neofiber*. The interparietal is squarish in outline and usually somewhat

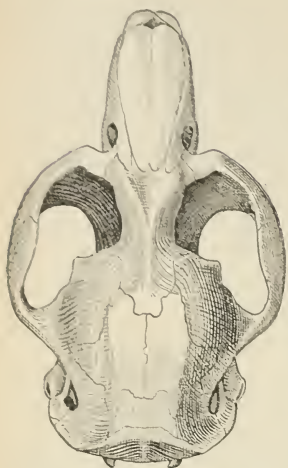


FIG. 37.—Skull of *Fiber zibethicus* (natural size).

longer transversely than antero-posteriorly.

Teeth.—The molars are all rooted in the adults (fig. 38), though the roots on the back lower tooth are usually less well developed than those on the others. Otherwise the teeth are exactly as in *Microtus*. The enamel pattern (fig. 39), most closely resembles that of *Microtus (Neofiber) alleni*, but differs in the larger anterior loop of the first lower molar. This loop is cut by two deep reentrant angles, which often isolate two additional closed triangles, making seven in all.

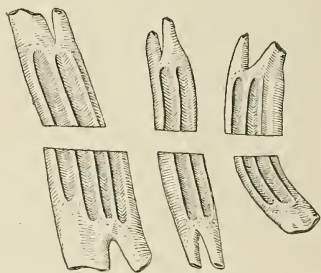


FIG. 38.—Side view of molars, *Fiber zibethicus*. ($\times 1\frac{1}{2}$.)

Feet.—The feet are large and so formed that they can be turned edgewise when carried forward, thus producing the least possible resistance to the water while the animal is swimming.

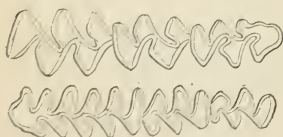


FIG. 39.—Enamel pattern of molar teeth, *Fiber zibethicus*. ($\times 2\frac{1}{2}$.)

This character is, however, to a certain extent, reproduced in the more aquatic species of *Microtus* and can not be considered diagnostic of *Fiber*.

Miscellaneous characters.—The tail is strongly compressed laterally, making an effective rudder. The peculiar form of the tail is scarcely noticeable in the young even when large enough to leave the nest, but develops rapidly as the animals increase in size.

The fur of the species of *Fiber* is highly modified to produce a

thoroughly waterproof covering. The long hairs are remarkably close and glossy, while the under fur is very dense. In the character of the fur *Fiber* is approached by some of the aquatic species of *Microtus*, especially *M. (Arricola) terrestris* and *M. (Neofiber) alleni*.

General remarks.—*Fiber* is very closely related to *Microtus*, from which it is distinguished by its flattened, rudder-like tail and rooted molars.

In addition to the well-known musk rat, *Fiber zibethicus*, three forms, whose interrelationships are not yet understood, are now recognized. These are: *Fiber zibethicus pallidus* Mearns, *F. obscurus* Bangs, and *F. ricalcius* Bangs.

DESCRIPTIONS OF EXTINCT GENERA AND SUBGENERA.

Three extinct rodents referred by authors to the family *Microtinae* have been made the types of superspecific groups. Two of these, from the Postpliocene of Pennsylvania, are subgenera of *Microtus*; the third, from the Quaternary phosphorites of Trara de Nédroma, near Ain-Mefta, Tunis, is a genus of doubtful affinities. As these groups are necessarily based almost wholly on dental characters, it is impossible to describe them in the same manner as the living genera and subgenera. It is furthermore impossible to form a clear judgment of the validity of the groups in question without examination of the actual specimens. Such examination I have not been able to make. Hence the few conclusions here reached are necessarily incomplete and unsatisfactory.

The genus *Bramus* Pomel (*Comptes Rendus*, Paris, CXIV, p. 1159, 1892), from the Quaternary Phosphorites of Tunis is represented by one species, *Bramus barbarus* Pomel. Of this animal the mandible and the teeth of both jaws are known.¹ These show characters which suggest the *Castoridae*.

¹ Les molaires montrent sur leur couronne la structure de celles du rat d'eau, dont elles ont à peu près les dimensions. On y voit une double série d'encoches et d'angles alternatifs qui correspondent latéralement à des arêtes saillantes, 5 en dedans et 4 en dehors à la première dent inférieure, 3 de chaque côté aux deux suivantes inférieures et aux deux premières supérieures et 2 seulement avec arête postérieure à la troisième d'en-haut. Chez *Arricola* cette dernière est beaucoup plus compliquée, ayant trois paires d'arêtes et un fort contrefort postérieur. Dans la fossile les sillons sont moins profonds, à angles moins vifs, ainsi que les arêtes, et les lignes d'émail ne se soudent pas d'un côté à l'autre de la couronne, ainsi qu'elles le font chez *Arricola*; il en résulte une ligne médiane continue de dentine sur la couronne, au lieu d'une série alternative de petits triangles bordés d'émail; de sorte que la dent d'*Arricola* est, en réalité, formée de deux rangées de prismes distincts, tandis que celle du fossile est un prisme unique fortement sillonné sur les côtés. Il y a plus de ressemblance avec certains Gerbilles, qui ont cependant les molaires bien moins prismatiques et autrement constituées.

Les molaires des *Arricola* ne sont jamais radiculées sauf peut-être chez les très vieux sujets. Dans notre fossile, je les ai trouvées toujours radiculées dès qu'elles percent l'alvéole dentaire; leur fût, quoique franchement prismatique, est bien moins allongé. Ses deux racines, à la vérité, sont très longtemps ouvertes à leur extrémité,

The molars, which are rooted, do not differ essentially in enamel pattern from those of living species of *Microtus*, except that the back upper tooth is remarkably simple in structure, and the reentrant angles in all the teeth are so shallow that the triangles are open. While the front lower molar has nine salient angles, as in typical *Microtus*, the posterior maxillary tooth has only four and a very small terminal loop. The author remarks that the open triangles give the teeth of *Bramus* a resemblance to those of some of the *Gerbillidae*, but this likeness must be very superficial. The most remarkable character of *Bramus* is the form of the mandible, which is like that of *Castor* and very unlike that of any of the *Muridae*. It is probable that *Bramus* is the type of a group differing too widely from any of the recent *Microtinae* to be united with them in one subfamily.

The subgenera *Isodelta* and *Anaptogonia* were described by Prof. E. D. Cope in 1873 (Proc. Amer. Philos. Soc., XII, p. 87). Both are based on teeth from the Postpliocene deposit in Port Kennedy Cave, Pennsylvania. *Anaptogonia* is very different from any of the living subgenera of *Microtus*—so different that, as Professor Cope suggests, it may be eventually recognized as a distinct genus. *Isodelta*, on the other hand, is hardly separable from *Pitymys*, since the characters pointed out as diagnostic of the two groups are not beyond the range of variation among the species of one subgenus.

The original description of *Microtus hiatidens*, the type of the subgenus *Anaptogonia*, is as follows:

Represented by several molar teeth. These are several times as large as the teeth occupying the same position in any of the species already mentioned in this essay, and suggest the genus *Fiber*. The distinctive features of the latter are the compressed, oar-like tail, with rooted molars, and it is evident that the relationship of this species is not to it. Perhaps it is neither an *Aricola* (sic.) [= *Microtus*] nor a *Fiber*, since it differs in the structure of the teeth from the known species of both. None of the triangles are isolated, but are connected by a narrow strip of dentine, which is narrow posteriorly, but widens anteriorly until it opens out into the terminal loop. Thus the sectional name *Anaptogonia* may be found ultimately applicable to a separate genus. The separation of the enamel folds merely carries to the highest degree that which is seen in the anterior part of the tooth of *A. sigmodus*.

In the inferior m 1 the triangles, which do not open on one side to the anterior loop, are $1\frac{1}{2}$, then one on each side, and the short, wide, terminal loop, which is bilobed or emarginate in the middle of the end. The ridges, which are very prominent and acute, are, therefore, $\frac{5}{8}$; at the extremity there are two short ones, between

mais elles sont de bonne heure parfaitement distinctes l'une de l'autre. La troisième molaire inférieure, un peu plus arquée que dans *Aricola*, ne descend pas à la face interne de l'incisive, mais reste tout à fait au-dessus, et ses racines seules s'insinuent un peu latéralement sur cette face.

L'os mandibulaire présente des différences beaucoup plus importantes. Son apophyse angulaire, restant presque dans le plan général de l'os, ne fait en arrière qu'une légère saillie bordant la branche montante, qu'elle suit très haut sous le condyle pour se terminer en simple petit cran. Il y a une grande analogie de forme avec ce que l'on voit chez les Castors. Dans *Aricola*, au contraire, l'apophyse angulaire est basse et se rejette obliquement en arrière en forme de euilleron fortement crochu et tordu, rappelant du reste, sauf cette torsion la disposition de cette partie chez les autres Muridés.

which a third and more prominent one rises a little below the grinding surface. A little more attrition would give the distal loop a trilobate outline, and a little more, an acuminate one, from the loss of the lateral angles; finally the median ridge disappears also.

The subgenus *Isodelta* is considered by Professor Cope to show an exaggeration of the characters of *Pitymys*. The type and only known species, *Microtus speothen*, is described as follows:

This species is represented by the entire dentition of the left ramus mandibuli, with a few fragments of the adjacent bone. As already pointed out, its characters entitle it to rank as a distinct section of the genus. Thus, the triangles of the inner side of the anterior inferior molar are one less than in any species of the section *Arvicola* [= *Microtus*]. The anterior loop presents two well-marked angular basal areas, while its terminal portion is regularly rounded. * * * That this is not one of the species of *Pitymys*, in which the basal lobe of the anterior trefoil has been cut off by unusual inflexion of the enamel angle, is demonstrated by the structure of the second molar, which is precisely that of typical *Arvicola* [= *Microtus*], all the triangles from the posterior being isolated and alternating, producing the formula $1\frac{3}{4}0$. The third molar has the usual formula, 1-1-1, the posterior two lobes being crescentic, the anterior trapezoid.

NOTE ON ARVICOLA INTERMEDIUS NEWTON.

In a paper entitled 'The Vertebrata of the Forest Bed Series of Norfolk and Suffolk' Mr. E. T. Newton describes numerous remains of a microtine rodent with well-developed fangs on the molar teeth and intermediate in size between *Arvicola amphibius* [= *Microtus terrestis*] and the smaller voles. This animal, which Mr. Newton named *Arvicola intermedius*, has been recently referred to the genus *Phenacomys*.² While the species is certainly not an *Arvicola* [= *Microtus*], it appears to be equally far removed from *Phenacomys* and probably from *Erotomys* and *Fiber* also. The teeth are described as follows:

I have now before me about 40 vole jaws from the "Forest Bed" which, although differing somewhat in size, agree precisely in the patterns of their teeth. Only 14 of these allow the bases of their teeth to be seen, but nine of these have more or less distinct fangs; the other five have no fangs, but are most probably immature, as in other particulars they agree precisely. I have likewise some hundreds of isolated molar teeth, and a very large proportion of these are fanged. * * * The great variation in the size of these fanged teeth would lead one to suspect that they represent more than one species, but there are no sufficient grounds for their separation. * * * The patterns of the grinding teeth are so nearly like those of *A. amphibius* as scarcely to need description, and it is on the presence of fangs in the adult that the chief distinction between the two species rests; nevertheless, there are a few points deserving of notice. In one of the largest and most perfect mandibular rami (figs. 3, 3a) the entire molar series, measured along the alveolar margin, is 0.33 inch (8.5 mm.). Mr. Reeves's specimen, from the Bramerton Crag (fig. 12), is a little larger. The first molar has the five inner and four outer angles alternating, but the anterior two are not so prominent as is usually the case in *A. amphibius*, and the front of the tooth is somewhat more rounded (fig. 3b). In the Bramerton jaw this is especially the case (fig. 12a). All the anterior lower teeth from the "Forest Bed" series which I have seen have the infoldings of the enamel behind the anterior prism less deep than in those examples of *A. amphibius* which I have been able

¹ Memoirs of the Geological Survey, England and Wales. London, 1882.

² Nehring, Naturwissenschaftliche Wochenschrift, Nr. 28, July 15, 1894.

to examine; and hence the dentinal portion of the anterior prism is more widely confluent with the second inner and outer prisms; it is, in fact, an exaggeration of the form indicated by Blasius, fig. 186 (*Säugethiere Deutschlands*, p. 345). The second molar has three inner and three outer angles alternating. The third molar has likewise three inner and three outer angles, but the alternation of the prisms is so slight that the opposing inner and outer prisms are confluent. * * * I am not acquainted with any specimen which shows the three upper molars in place, but Mr. Savin has two specimens which retain the first and second upper grinders (fig. 1), and Mr. Reid has obtained several isolated specimens of last upper molars. The anterior upper molar (fig. 1a) has three inner and three outer angles alternating; the second tooth has three outer and two inner angles alternating. The third upper molars vary somewhat; in some only three inner and three outer angles can be counted (fig. 2a), while others have three inner and four outer angles. The widely confluent character of the front prisms of the lower anterior molar is repeated in these hinder upper ones. It will be noticed that in all Blasius's figures of the last upper teeth (l. c., p. 345) the anterior inner fold (cement space) and the two anterior outer folds extend across the teeth and meet the enamel of the opposite side, while in one case (fig. 190) the two inner folds pass across. Now, in most of the teeth under consideration it is only the one anterior inner and one anterior outer fold which pass across; in some instances the second outer fold passes farther inward, but I do not think that in any instance it touches the opposite side.

The teeth of '*Arricola intermedius*' differ in numerous characters from those of *Fiber*, *Erotomys*, and *Phenacomys*, the only known living

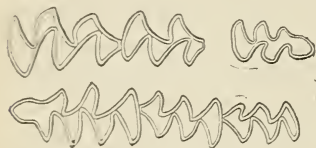


FIG. 40.—Enamel pattern of molar teeth, *Arricola intermedius*. From Newton.

microtines with rooted molars. The small size of the remains and the simple structure of the first lower molar are sufficient to indicate that the animal is not closely related to *Fiber*, although the character of the roots of the molars, as shown in figs. 5, 6, and 7 of Pl. XIII, is strongly suggestive of this genus. The figure of the inner

side of the lower jaw (Pl. XIII, fig. 3a) suggests that the posterior molar is strongly displaced by the shaft of the incisor, as in *Microtus*. This character alone would show that the species is neither an *Erotomys* nor a *Phenacomys*; but the peculiarities of the enamel pattern furnish additional reasons for its exclusion from these genera. The enamel pattern (fig. 40) is, as Mr. Newton remarks, almost exactly like that of *Microtus terrestris* (see fig. 34). It thus lacks the deep reentrant angles on the inner side of the lower molars characteristic of *Phenacomys*, and the rounded salient angles and opposite triangles characteristic of *Erotomys*. The last lower molar in particular is noticeably different from that of either *Erotomys* or *Phenacomys*. '*Arricola intermedius*' is apparently still further removed from *Erotomys* by the large size of the teeth as compared with the jaw. There can be little doubt that the animal represents a genus distinct from any now living.¹ In the absence of specimens, however, nothing would be gained by an attempt to name and define the group.

¹ Whether the rooted microtine teeth mentioned by Nehring (*Naturnissenschaftliche Wochenschrift*, Nr. 28, July 1894) and by Forsyth Major (*Atti Soc. Ital. Sci. Nat.*, XV, p. 389) belong to animals congeneric with *Arricola intermedius* is purely a matter of conjecture.

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[Synonyms in italics.]

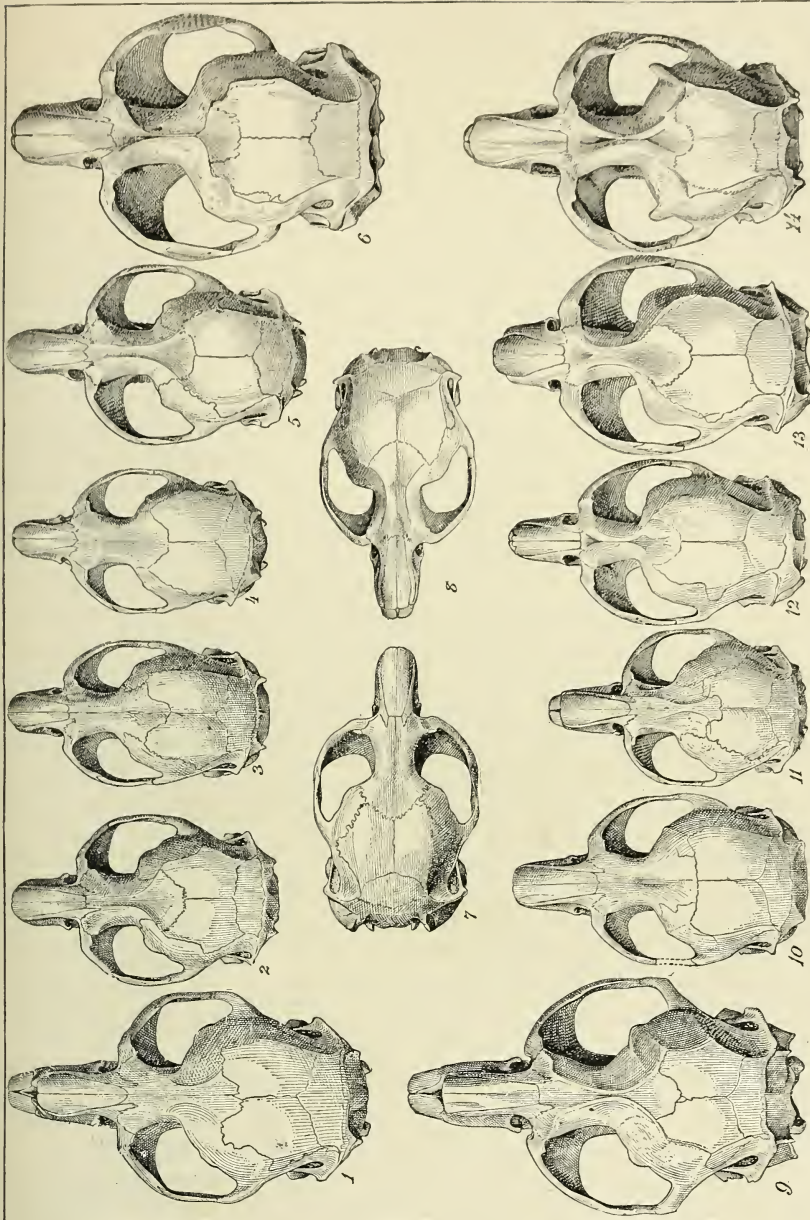
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PLATE I.

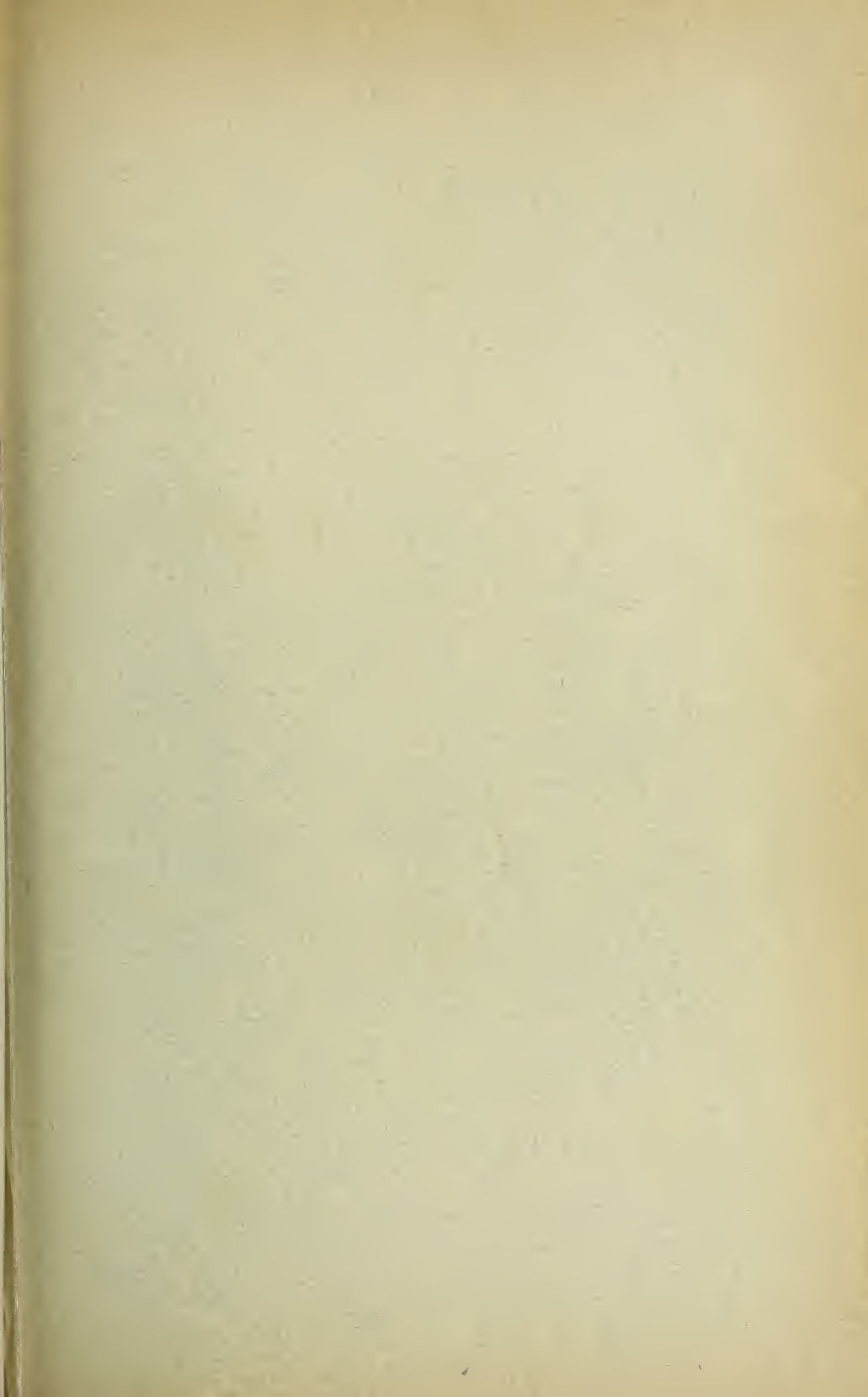
[Enlarged one and one-half times.]

- FIG. 1. *Microtus (Arvicola) macropus*. Wood River, Idaho.
(No. 31630, U. S. Nat. Mus.)
2. *Microtus (Pitymys) pinctorum*. Washington, D. C.
(No. 30332, U. S. Nat. Mus.)
3. *Microtus (Microtus) arvalis*. Cepin, nea. Esszek, Slavonia.
(No. 3035, collection of Gerrit S. Miller, jr.)
4. *Erotomys*. Portland, N. Dak.
(No. 35835, U. S. Nat. Mus.)
5. *Phenacomys oramontis* Rhoads. Mount Baker Range, British Columbia.
(No. 3562, collection of Gerrit S. Miller, jr.)
6. *Lemmus nigripes*. St. George Island, Alaska.
(No. 42680, U. S. Nat. Mus.)
7. *Microtus (Lagurus) curtatus*. Reese River, Nevada.
(No. 32498, U. S. Nat. Mus.)
8. *Microtus (Chilotus) oregoni*. Sumas, British Columbia.
(No. 4160, collection of Gerrit S. Miller, jr.)
9. *Microtus (Arvicola) terrestris*. Braunschweig, Germany.
(No. 1934, collection of C. Hart Merriam.)
10. *Microtus (Alticola) albicauda*. Type. Braldu Valley, Ballistan.
(No. 36916, U. S. Nat. Mus.)
11. *Microtus (Hyperacrius) fertilis*. Pir Panjal Range, Kashmir.
(No. 35511, U. S. Nat. Mus.)
12. *Synaptomys (Mictomys) wrangeli*. Wrangel, Alaska.
(No. 74720, U. S. Nat. Mus.)
13. *Synaptomys (Synaptomys) helalets*. Dismal Swamp, Virginia.
(No. 75172, U. S. Nat. Mus.)
14. *Dicrostonyx torquatus*. Petschora, Russia.
(No. 3621, collection of Gerrit S. Miller, jr.)



1. *Microtus macropsis*.
 2. *Microtus punctatorum*.
 3. *Microtus arvalis*.
 4. *Erotomys gapperi*.
 5. *Phenacomys oramontis*.
 6. *Lemmus nigripes*.
 7. *Microtus curtatus*.
 8. *Microtus oregoni*.
 9. *Microtus terrestris*.
 10. *Microtus albicauda*.
 11. *Microtus fertilis*.
 12. *Sturnomys arctagi*.
 13. *Sturnomys helictes*.
 14. *Sturnomys torquatus*.





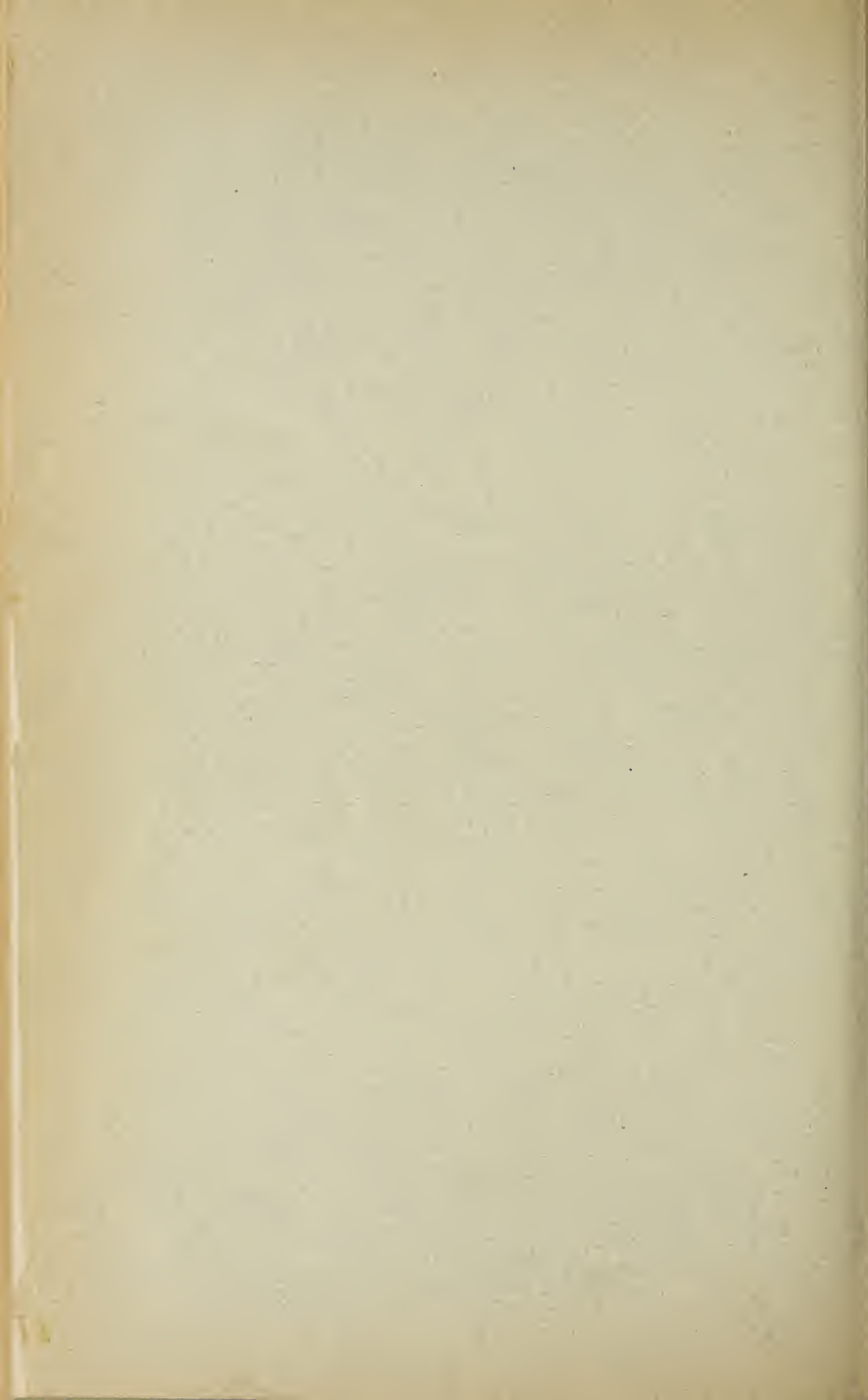
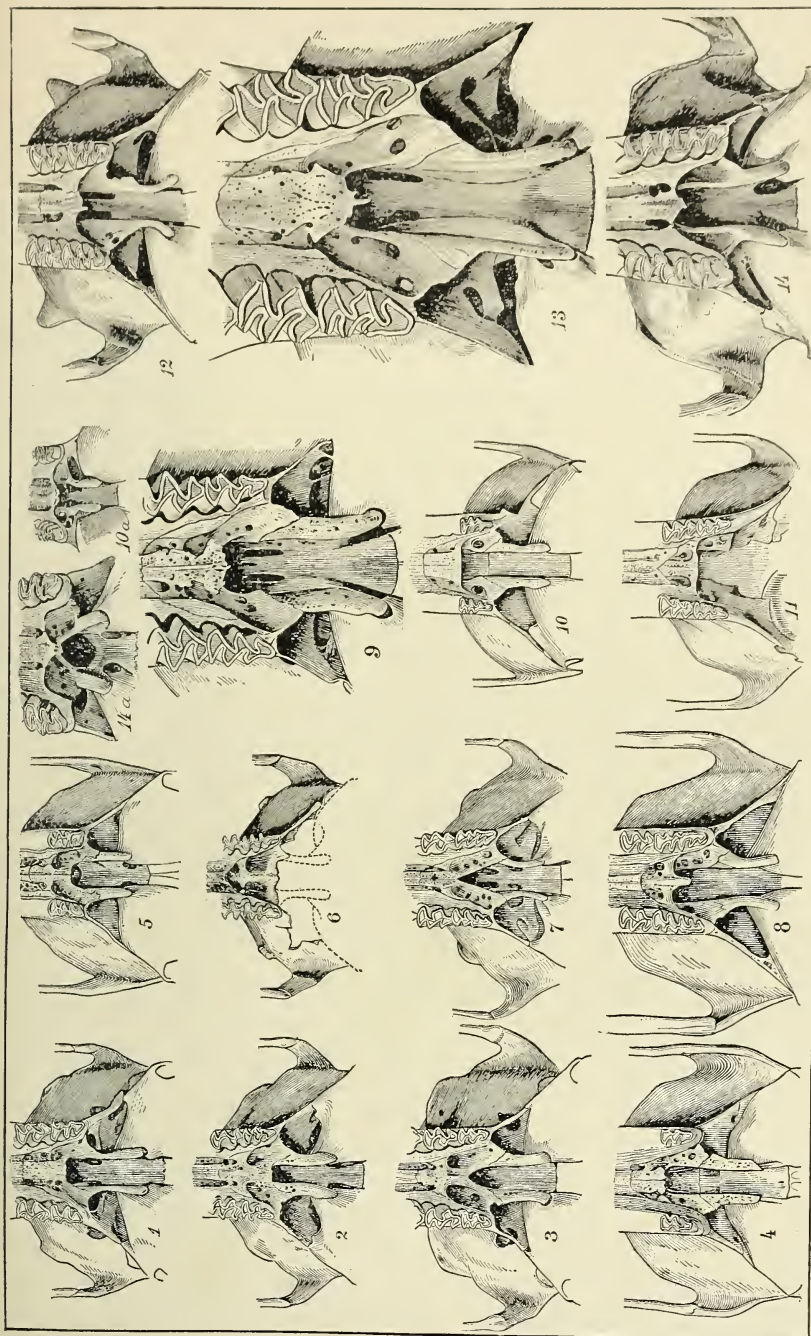


PLATE II.

[Enlarged two and one-half times.]

- FIG. 1. Bony palate of *Phenacomys*. Salmon River Mountains, Idaho.
(No. 31249, U. S. Nat. Mus.)
2. Bony palate of *Microtus (Lagurus) pallidus*. Reese River, Nevada.
(No. 32498, U. S. Nat. Mus.)
3. Bony palate of *Microtus (Pitymys) pinetorum*. Washington, D. C.
(No. 30332, U. S. Nat. Mus.)
4. Bony palate of *Microtus (Alticola) blanfordi*. Nultar Valley, Kashmir.
(British Museum Register, 81. 3. 1. 23.)
5. Bony palate of *Microtus (Microtus) arvalis*. Geneva, Switzerland.
(British Museum Register, 79. 9. 25. 52.)
6. Bony palate of *Microtus (Lagurus) lagurus*. Gurjeff, Russia.
(No. 3619, collection of Gerrit S. Miller, jr.)
7. Bony palate of *Microtus (Arvicola) arricoloides*. Type. Lake Kichelos, Washington.
(No. 1358, collection of S. N. Rhoads.)
8. Bony palate of *Microtus (Antelionys) chinensis*. Type. Western Sze-chuen, China.
(British Museum Register.)
9. Bony palate of *Microtus (Neofiber) alleni*. Florida.
(No. 23452, U. S. Nat. Mus.)
10. Bony palate of *Eutamias glareolus*. Christiania, Norway.
(British Museum Register, 84. 10. 31. 11.)
10. View perpendicular to plain of palate.
- 10a. View from below and behind at strong angle with plain of palate.
11. Bony palate of *Microtus (Eothenomys) melanogaster*. Western Fokien, China.
(British Museum Register, 92. 10. 12. 52.)
12. Bony palate of *Dicrostonyx torquatus*. Petschora, Russia.
(No. 3621, collection of Gerrit S. Miller, jr.)
13. Bony palate of *Fiber*. Lake George, New York.
(No. 67689, U. S. Nat. Mus.)
14. Bony palate of *Lemmus lemmus*. Vola. (From St. Petersburg Museum.)
(No. 3620, collection of Gerrit S. Miller, jr.)
14. View perpendicular to plain of palate.
- 14a. View from below and behind at strong angle with plain of palate.



1. *Phenacomys*,
2. *Lagurus*.

3. *Pitomys*,
4. *Alticola*.

5. *Microtus*,
6. *Lagurus*.

7. *Arvicola*,
8. *Antelomys*.

9. *Neofiber*,
10. *Eutamias*.

11. *Eutamias*,
12. *Dicrostonyx*.

13. *Fiber*,
14. *Lemmus*.



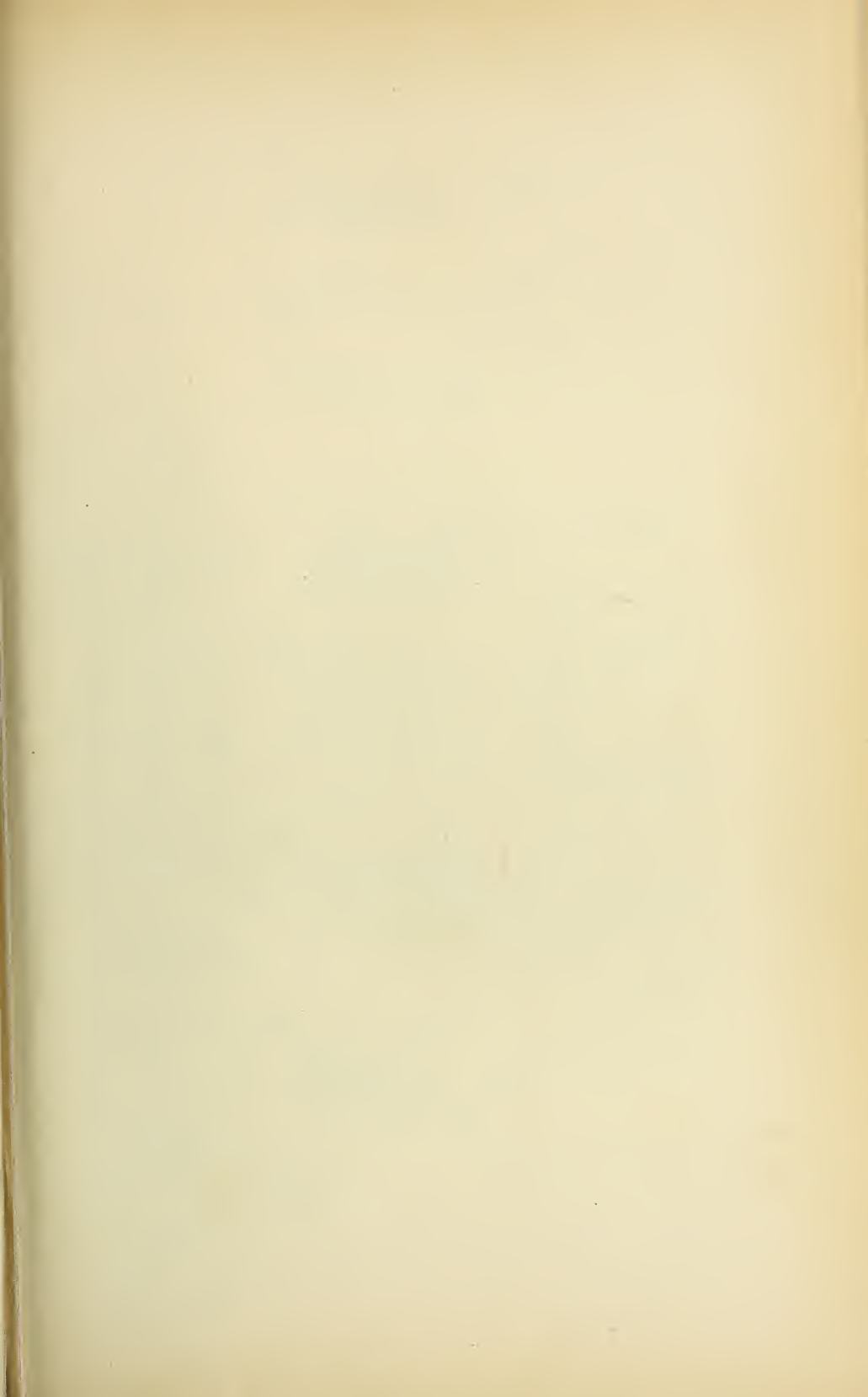


PLATE III.

[Enlarged two and two-thirds times.]

FIG. 1. *Synaptomys cooperi*. Roan Mountain, North Carolina.
(No. 50865, U. S. Nat. Mus.)

1. Left mandible from beneath; bone cut away to expose roots of teeth.

1a. Left mandible from inner side; bone cut away to expose roots of teeth.

2. *Phenacomys oramontis* Rhoads. Mount Baker, British Columbia.

(No. 3562, collection of Gerrit S. Miller, jr.)

2. Left mandible from beneath; bone cut away to expose roots of teeth.

2a. Left mandible from inner side; bone cut away to expose roots of teeth.

3. *Microtus pennsylvanicus*. West Tisbury, Mass.

(No. 1885, collection of Gerrit S. Miller, jr.)

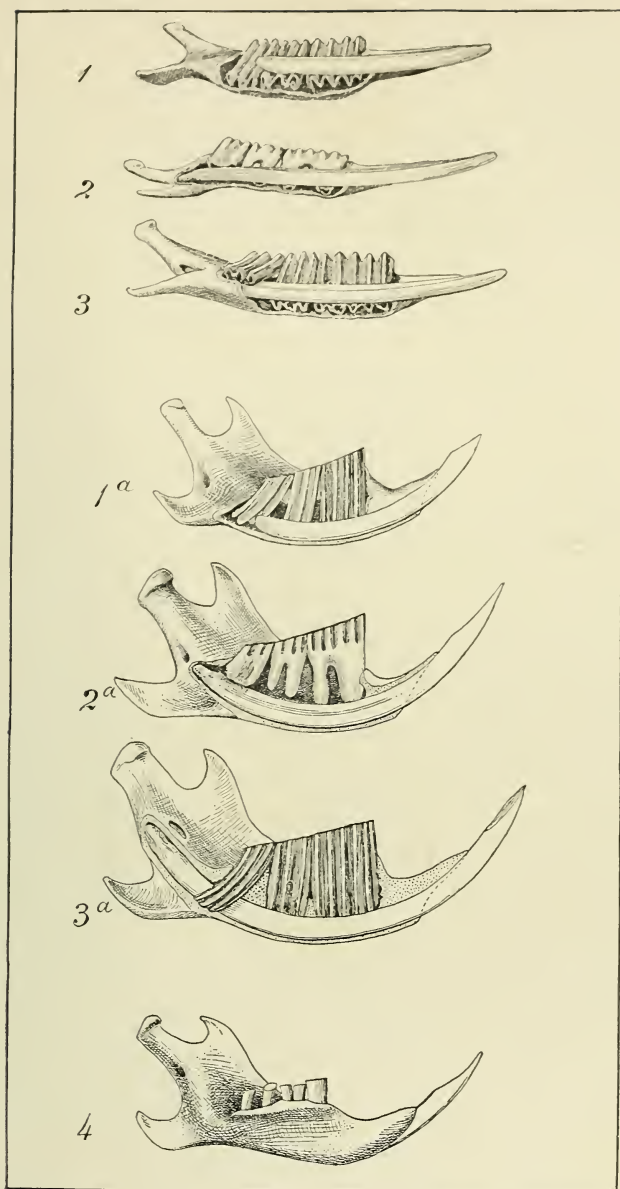
3. Left mandible from beneath; bone cut away to expose roots of teeth.

3a. Left mandible from inner side; bone cut away to expose roots of teeth.

4. *Erotomys gapperi*. Seekonk, Mass.

(No. 193, collection of Gerrit S. Miller, jr.)

Left mandible showing effect of excessive wear on teeth.



1. *Synaptomys*.
2. *Phenacomys*.

3. *Microtus*.
4. *Erotomys*.

